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CONCEPTS OF HOMOLOGY AND ANALOGY[1]

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ALAN BOYDEN (1943) has done biology a good service by reviewing the history and the conceptual significance of the terms homology and analogy. Having arrived at somewhat different conclusions and other viewpoints in going over much the same ground in 1926 and 1937 (unpublished reports), I venture now to enter the discussion.

EVOLUTION OF THE HOMOLOGY CONCEPT

With abounding respect for the master anatomist, Boyden recommends that we return a full hundred years to Richard Owen's pre-evolutionary concepts and definitions of homology and analogy. This recommendation obviously did not stem from any belief that the law of priority holds for concepts, but rather from Boyden's conviction that Owen's 1843 definitions remain precise, clear and adequate. That, they indeed were, in Owen's day. But the ideas of homology and analogy have evolved through a century of vast advances in biology, so that it is now difficult in some respects to trace the homology of ideas. During the same period most of the major concepts of biology have become fundamentally modified. Think of "evolution," of "mutation," of "species."

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The homology concept has undergone a great, but not yet complete change, from static to dynamic. Traditional meanings and limitations have held on, at times with the effect of confusing ideas and retarding progress.

In its original form the homology concept pertained only to structures, as they are independently manifested in the adults of different animals (or plants). It called for correspondence in position, in agreement with the mathematical concept of homology, and for similarity in fundamental structure. Owen's idea of agreement in position and structure, indicating "the same organ in different animals under every variety of form and function," anticipated the theory of common descent with modification, and took on vastly greater significance as the theory of evolution became the dominant interpretation of biology. As a result the homology concept became and has ever since remained a potent one in evolution, and also in embryology and in modern systematics, as well as in comparative anatomy.

Homology has thus come to signify an agreement in evolutionary derivation, and, either as a corollary or as a prime criterion (Haeckel), an agreement also in embryonic development. Proof of homology has become the basis of phylogeny. The ideas of homology and community of origin have become intimately associated, almost to the point of synonymy. This association has perhaps gone a bit too far, for fundamental agreement in structure and in mode of ontogenetic origin does not always involve a common phyletic origin. We will revert to this point later (p. 300).

PERTINENCE OF HOMOLOGY TO FUNCTIONS AS WELL AS STRUCTURES

The original limitation of the homology concept to structures has been most unfortunately persistent. Acceptable only from the standpoint of static morphology, this limitation is undesirable in its effects and illogical in the modern view: undesirable, because it maintains an

overemphasis on structure as a tool of evolutionary and taxonomic research; and illogical, because systematists and geneticists are dealing more and more with physiological as well as morphological characters and because biologists have come to recognize the inseparability of structure and function. Conklin (1943: 105) well expresses the current viewpoint: "No postulate of biology is more certain than this, that the functions of life are inseparably associated with the structures of living matter. This is a conclusion of the utmost importance in biology and philosophy."

Since homology has become a basic evidence of evolution, its continued limitation to structures seems incongruous. It is common understanding that function and structure yield like evidence regarding relationships and ought to be considered on the same terms.

It is recognized, to be sure, that functions are repeatedly subject to convergent evolution, both progressive and degenerative, but all biologists would now agree that this is also true of structures. Superficial likenesses in functions—mere uses—often arise independently, but so also do superficial resemblances in structures. In either case we deal with analogies rather than homologies. Fundamental similarities in the "intrinsic functional mechanism" are properly regarded as a criterion of homology (Tait, 1928)—as valid a criterion as that furnished by deep-rooted agreements in structure. Tait clearly detailed the fundamental similarities in the physiology of homologous organs, particularly those of internal secretion (but of course went too far in insisting that homologous organs never change their intrinsic functions; consider, for example, the modification of the anal fin in the males of poeciliid fishes to form the intromittent organ). The problem of the homology of certain organs may therefore be subjected to physiological test.

Along with the associated structures, functions having as their chief attribute use rather than biochemical properties may also be indicative of homology. Thus the

reflexes and behavior patterns responsible for the flight of two birds possess an evolutionary significance directly comparable to the structural agreement or homology that exists between the wing of the first bird and the wing of the second. The clawing of a cat and of a tiger has much the same meaning as does the homology of the claws. Clawing may be independently evolved, and so may claws.

It is high time that we think and write of homologous functions in the same way that homologous structures have been treated, and that we discard from the definition of homology any necessary restriction to anatomy. Many biologists, I am sure, have thought in such terms. Certainly developmental homologies are conceived in terms of genetically consistent processes quite as much as in terms of the structure, either of the genes or of the final product. And surely every finished organ involves functions just as much as it does structure.

The limitation of the homology concept to structures is perhaps more a function of the stated definitions than of thought, but the definitions do have an effect on concepts and applications. Some biologists whom I have consulted seem surprised or confused at the limitation expressed in recent definitions. As an apparently fair sample we may take the biological definition of homology in Webster's New International Dictionary (second edition):

> Correspondence in type of structure between parts or organs of different organisms due to differentiation by the process of evolution from the same or a corresponding part or organ of some remote ancestor; also, true correspondence in type of structure between different parts of the same individual. Distinguished from *analogy*, or resemblance in function (or sometimes also in form) between organs of different origin.

Though the modern evolutionary meaning of homology is given full emphasis in this and similar definitions, we still find the limitation to structure. Perhaps the next revision will read, "structure or function."

ATTEMPTED RESTRICTIONS OF THE HOMOLOGY CONCEPT

Boyden would have us divest homology of its expanded meanings, and in particular urges that we dissociate

"serial homology" (for which he in part adopts Owen's little-used term, "homotypy") from "true or special homology." Boyden stresses the claim that correspondences in structure are much closer in special homology than in "homotypy," illustrating his points by a comparison of the appendages of two crustaceans, *Homarus* and *Callinectes*. Further consideration, however, shows that serial homologs are often much more alike than are some special homologs. Thus pereiopods 2 and 3 of the lobster are more similar to one another than either one is to the corresponding leg of the blue crab. As a whole the lobster's pereiopods are terete; the blue crab's, compressed. In some crustaceans all the walking appendages are short; in others, greatly elongate. Such resemblances in serial homology are presumably due to a common genetic basis and may therefore be used (contrary to Boyden's claim) as evidence in phylogenetic research; they surely have the same sort of evolutionary significance that other types of homology furnish. Broadening comparisons, we often find vastly greater correspondence in anatomy, and in homology, between serial structures in one individual than between the "same" structures in two animals. Thus we see vastly greater agreement in fundamental structure and relationships of parts when we compare the fore limb and the hind limb of a horse, than we do when we contrast the fore limb of the horse with its special homolog, the pectoral fin and girdle of a teleost fish.

It seems unwise to restrict the homology concept to special homology, that is, to the relationship between specifically corresponding structures of different individuals. The wisdom of the broader concept becomes especially clear when we consider the homology between structures which are dispersed at random, or which form elements of a pattern, in which few or none of the individual elements can be homologized with individual elements in another animal. Take scales, for example. It would be a slap at almost any basic concept of homology, to deny, on some

arbitrary distinction, that any scale of one teleost, say a trout, is homologous with any scale of another teleost, for example, a herring, even though no one scale over the general body surface of a trout can be specifically homologized with any one scale on the herring. More definite homologies arise when certain scales, associated with fins and with head structures, become particularly specialized. Such scales include the elongate pelvic axillary scale in many fishes, the non-imbricate scale on the top of the head in cyprinodont fishes, and primitively, the scales which in early fishes became modified to form particular membrane bones. Special importance is attached to the homologies between these particularized scales, but there is significance also in the general homology between the non-placoid scales of certain types, and in the lack of homology between placoid scales and cycloid scales.

It seems even more illogical to restrict the concept of homology to structures in different individuals. If we admit the homology between any scale x of an individual trout and any scale, say y, of a salmon, and between this scale y in the salmon and scale z in the trout, then how can we logically deny that homology exists between scales x and z on the body of the same trout?

Considering the original structure of scales leads us to question again the advisability of excluding correspondences in serially segmented structures from the scope of homology. All non-placoid scales seem to possess at least a generalized homology, although in evolutionary origin they are to be interpreted as segmental structures, that is, as articulations in the hardened exterior of each myomere.

Peter (1922) went so far as to urge that the homology concept be restricted to structural agreements between species and higher groups, disregarding the similar structural correspondences between individuals of one species as well as the homologies between parts of the same individual.

The idea has even been suggested that the concept of homology should be applied only to the broader corre-

spondences between the larger groups of organisms. But the principles of phylogeny which pertain to the greater divisions hold in large part for the lesser groups, such as species and genera. Furthermore, there is quite as much need for interpreting homologies between the diagnostic characters of the minor groups as there is for interpreting the evolutionary relationships between the characteristics of the major groups.

Many abortive attempts have been made to narrow the homology concept. The great biological theorist Ernst Haeckel was one of the first to attempt a restriction of the term homology to correspondence between structures of two individuals. For the equivalence of structures in the same organism he concocted two new terms, "homodynamy," applying to structures appearing serially in successive metameres of the body; "homonymy," for structures aligned along secondary axes of the body. So far as I know he proposed no term to cover the generally underemphasized relationship between structures, like hair or scales, that are more or less diffusely distributed over the body. Later, Spemann (1915) proposed that the abandoned term "homonymy" be applied to these relationships between diffuse structures. Richard Hertwig used the term "homonomy" in the sense in which Haeckel had employed "homodynamy"; Gegenbaur followed Haeckel's usages, except that he adopted the spelling "homonomy" in place of "homonymy" and expanded the concept to include the relationships of serially arranged structures within one portion of the main axis of the body.

In one of the better known attempts to restrict the homology concept E. Ray Lancaster (1870) regarded as truly homologous, or "homogenetic," only those corresponding structures which can be traced to a single representative structure in some common ancestor. In contrast, similar structures that result from the action of like forces were called "homoplastic." At first Lancaster restricted the application of the term "homoplasy" to comparable modifications of similar and generally homolo-

gous structures. In this sense homoplasy would correspond fairly well to the relation between "independent homologies" (p. 300). But later he expanded the concept to apply to changes resulting from the action of like forces on any structures, whether homologous or non-homologous. In the end, therefore, Lancaster merely substituted "homogeny" for special homology and "homoplasy" for analogy. His idea of "homogeny" was akin to Haeckel's early concept of "homophyly."

The fact that biologists in general have not adopted such terms and have not followed such rather arbitrary distinctions suggests that neither the terms nor the distinctions may be of much value. The concept of homology has remained a broad one, as indeed it should.

In arguing for the unity of the homology concept I am not opposing the idea of classifying the types of homology. There would be many advantages in the fabrication and use of such a classification, but it would seem wisest to call all the types homologies, specifying the kinds by adjectival prefixes.

Inconsistencies without end would arise from the application of suggested restrictions of the homology concept and of the associated terminologies. Thus, according to some, my left arm is not homologous with my right arm, nor is the left pectoral fin (and girdle) of a fish the homolog of the right fin of the same fish, although my left arm is homologized with the left pectoral of the fish. What some of the concept splitters would have done with diffuse structures like scales, or with resemblances between the successive proglottids of a tapeworm or the segments of an annelid is hard to guess. Would they homologize parapodia or nephridia only in segments that are demonstrably of specific common origin?

If we should consistently exclude right-left, serial and diffuse structures from the homology concept we would ignore many fundamental agreements (*i.e.*, homologies) in phylogenetic and ontogenetic development. To restrict homology to organs or parts that have a specific common ancestral structure would assume modern meaning only

if specific sets of genes could be shown to be specifically responsible for the independent development of each structure—which of course would be contrary to the present conclusions of genetics.

It seems to me that the only serviceable modern concept of homology is that of the essential genetic agreement of structures and functions in evolutionary derivation and in embryonic development.

Complexities in Homology

On this or almost any other broad concept homologous relationships involve many complexities. In the first place, there may be many degrees of specificity in homology. Two characters may be homologous from one point of view but non-homologous from another viewpoint. As units of organic structure all cells are homologous, but as units of hepatic tissue, only part of the cells of one animal are homologous with those of another individual. As a vertebrate limb a bat's wing is homologous with a bird's wing, though as a wing it is only analogous. As basic elements of the exoskeletal armor each membrane bone in the skull possesses a generalized homology with every other membrane bone and with each non-placoid scale, just as any ordinary scale is homologous with any other scale (of the same or another individual); but any one membrane bone can be rigidly homologized only with the same bone in another individual (or with a bone on the opposite side of the same animal). By general agreement the teeth of all vertebrates from elasmobranch to mammal are homologous with all denticles on the body surface of any elasmobranch, but as a tooth, any vertebrate tooth is homologous only with other teeth. As a certain type of tooth, the mammalian molar, to cite an example, is homologous only with other true molars. Individually specialized molars are homologous only with the corresponding tooth in another mammal or on the other side of the jaw in the same individual. Where to draw the line in interpreting homologies is a function of the special needs in any comparative study. It is not logical, how-

ever, to exclude from the homology concept any structures which have a true agreement in derivation—of the degree and sort indicated by the comparison being made.

Many complexities in homological relationships come to mind when we review the facts of anatomy and variation. Thus the membrane bones shift from the exoskeleton to the endoskeleton, to become covered by unmodified scales; when accessory scales are developed, the homologs come to lie three deep. Similarly, the lepidotrichial elements of the fin rays take on new structural relationships and to this degree outgrow their basic homology with scales; like membrane bones, the fin rays may become covered with ordinary scales. Nature's faculty for overriding regular rules is exemplified by the development of a new pair of horns alongside the old pair in four-horned goats and sheep; also by homeotic variations; and by the almost identical modification of non-homologous structures. Such irregularities, however, encumber almost all biological concepts, but destroy neither their validity nor their usefulness.

Perhaps even more serious difficulties beset the homology concept when we try to express homologies in terms of genetics. Individual genes have multiple effects, and a given character may be affected by many genes. Similar results may be effected by different genes or combinations of genes. Mutations greatly modify the genetic mechanism. Modifying genes come and go. Some homologous mutations are virtually identical in fundamental nature and in effect; others are more or less different. "Systemic mutations" (Goldschmidt, 1940), which greatly reorganize the hereditary complex, are not to be wholly excluded. What degree of genetic integrity is to be required for the interpretation of homology? How complete must the genetic analysis be, to warrant such interpretation? In many cases how can we feel any assurance as to the fundamental agreement of corresponding structures, in terms of the genetic mechanisms involved? Some geneticists have gone so far as to decry

the significance of homologies, but Boyden (1935, 1943) has plausibly refuted such destructive views and has indicated that homology may still be regarded a genetic phenomenon.

Boyden (1943) stresses the increasing uncertainties that pertain to homological interpretations, as we shift our attention from forms capable of interbreeding to those progressively less closely related. I feel inclined to emphasize the special difficulties that arise in interpreting the homologies between the characters of very closely related forms. In the first place the genetic background within minor circles of evolution must be greatly complicated by the processes of reticulate evolution (stressed by Dobzhansky, 1941, and by Huxley, 1943). In the second place the frequency of parallel evolution among related forms—attested by a great mass of speciational evidence—often makes it impossible to decide whether or not detailed agreements are due to common origin. How then can we objectively interpret the homology of such characters? Homologies in phylum, class, order and family characters are commonly much more obvious and secure than are the homologies in generic, specific and subspecific characters.

Still further complications arise when we try to reconcile the facts of experimental embryology and regeneration with the homology concept. The regeneration of an antenna in place of an excised eye in crustaceans has long been a puzzle from the viewpoint of homologies. Knowledge of organizers, fields of growth and of differentiation, of axial gradients and of other developmental phenomena interposed between the gene and the specific adult, can hardly be said to have simplified the concept of homology. These considerations force us to treat homology with less extreme precision than was once demanded. For example, the third anal ray of the adult male in poeciliid fishes, such as *Gambusia*, has certain highly characteristic structural modifications. These same features appear on the fourth ray, if the third ray during development be excised

at the base (Turner, 1941). Under these conditions the field of differentiation can operate on the fourth ray. We are finding that these and other gonopodial features in the poeciliids seem to owe their expression to position: structures normal to the anterior edge of the gonopodium normally develop there on ray 3, but will appear on ray 4 if that ray forms the front margin; other special structures that normally develop on the posterior edge of ray 4 or of ray 5 will develop on other rays if these rays by reason of malformation or operation present a free posterior edge. Obviously, such characters do not arise *de novo*. They may surely be regarded as homologous with the normally manifested structures, though they appear on new parts (different rays) or in duplicate (on two or more rays instead of one).

Transformation of one type of structure into a distinct type may occur in the process of normal development as well as in regeneration. A noteworthy example is the change with age of the third anal ray in certain fishes, for example *Mugil* (Jacot, 1920: 207–208), from a flexible, articulated, bilaterally paired soft ray into a robust, bony, pungent, non-articulated, solid spine. It is doubtful that spines are homologous with soft rays, except in a very general sense, yet here we find what appears to be a true spine developing out of a soft ray. The field for spine formation appears to move backward far enough to involve an additional ray. The transformed structure is surely not a *de novo* development. It must result from the same developmental factors as other spines. It is therefore more closely and certainly homologous with the other spines than with the soft ray out of which it was transformed.

INDEPENDENT HOMOLOGIES

Ineradicable complexities seem to be inherent in certain relations which perfectly fit Owen's concepts of homology but do not completely qualify under the evolutionary concept of homology. For many years such relations have perturbed students of evolution. They were apparently

prominent in Lancaster's mind when he first (1870) proposed the term homoplasy to designate the similar but independent modification of homologous structures. Referring to the independent origin of morphologically similar cusps on homologous teeth of different mammals, Osborn (1907) concluded that we "deal with homology, or more strictly with a *principle intermediate between homology and analogy.*" We can find, in fact, a full transition between homologies and analogies.

Detailed analyses in systematics, in comparative anatomy and in animal behavior often reveal examples of the identical but independent modification of homologous structures or behavior patterns. There may be full agreement in all morphological or behavioristic relationships and in ontogeny. In such circumstances all criteria of homology may be met, except that of a single, continuous lineage. Good circumstantial evidence indicates, to take one example from our own studies, that bifid teeth and intestinal coils of a certain type have been evolved repeatedly in the Goodeidae, a family of cyprinodont fishes (Hubbs and Turner, 1939). In the Clupeidae, as a second example, a peculiar type of raker-lined pocket has been developed, again and again we feel sure, by an extension and evagination from the upper anterior end of the fourth gill-slit (Hubbs and Lagler, MS). The end results of such parallel evolution may be scarcely distinguishable on any morphological, physiological or developmental grounds. Are they homologous? On the basis of essential similarities and of mode of development in the individual we may answer "Yes"; on the basis of monophylety, we could say "No." I prefer to compromise by calling such relations "independent homologies," despite the apparent contradiction in the term. Some may care to use a special term for such relations, and perhaps will choose "homoplasy" (employing Lancaster's term in the original rather than the modified definition—see p. 295), or "homomorphy" (Fürbringer, Gegenbaur), or "rectigradation" (Osborn, 1907). The fundamentally impor-

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tant general consideration is to recognize that conditions intermediate between homology and analogy exist. In each case the significant things are to understand the relations involved, to make clear what doubts or unsolved interpretations remain and to specify what is meant by the terms used.

The same or a similar modification of homologous attributes may occur on convergent or divergent as well as on parallel lines of evolution, and in distantly as well as in closely related groups. Evidence keeps accumulating, however, to indicate that such independent homologies are particularly characteristic of closely related lineages. Intrinsic as well as extrinsic factors are probably responsible for this circumstance. In related forms homologous genes are apt to develop homologous mutations. Certain physical or chemical features in the genes or in the constitution of the organism may predispose toward a given modification. Peculiar environmental relations, or evolutionary steps already taken in a certain direction, may give special advantage to a certain type of change. Finally there is the still unproved and inherently improbable though often asserted innate tendency to vary in a certain direction.

When the homologies or seeming homologies are within one evolutionary circle, it is often difficult or impossible to tell whether they arose monophyletically or polyphyletically. If the similar characters are polyphyletic in origin, in terms of time, they may or may not be the result of homologous mutations. But the precise genetic mechanism will seldom be known and will rarely be exactly identical. The more precisely we fix the prerequisites for the recognition of homology, the more difficult may the appraisal become. But the need for the best possible appraisal will remain.

In one sense almost all homologies are independent. In the most rigid interpretation a continuity between characters can occur along only those lineages which are maintained by certain types of asexual reproduction.

The complete turn-over of genes in each generation of sexually reproducing animals creates a minor discontinuity. A slightly greater discontinuity results when gene-determined characters skip one to many generations. Some characters, such as those which owe their expression to rare homozygous recessives, may appear very rarely. Still less frequent in expression may be characters that arise from independent homologous mutations. Characters which appear to have been totally lost for geological ages may still be represented by a hidden reserve of unexpressed genes. This becomes evident when we consider exceptions to Dollo's law of irreversible evolution, for instance, the reappearance of teeth in one isolated genus of anurans (Cornman, 1943). The development of ctenii on one highly specialized genus of poeciliid fishes may furnish another example. Surely the occasional reappearance of long-lost characters does not represent *de novo* development. Just what degree of genetic continuity is to be required for the identification of characters as homologous? Trouble lies in store for those who attempt to fix too precise limits, even when the genetic mechanism is thoroughly understood. Precision in concepts should not transcend the complexities that exist.

Concept of Analogy

Boyden urges that we return also to Owen's concept of analogy—but Owen like almost all subsequent authors seems to have wavered in his view as to whether analogy applies to all structures exhibiting like function or only to essentially unlike structures with one function. Owen's initial 1843 definition of "analogue," as quoted by Boyden, namely "a part or organ in one animal which has the same function as another part or organ in a different animal," would seem to exclude "homologues," which in contrast were defined, in the static view of pre-Darwinian time, as "the same organ." It seems probable that Owen first meant to apply the term analog only to organs that are not homologous. In 1848, however, as Boyden demon-

strates by a quotation, Owen admitted that homologs like the pectoral limb of porpoise and fish may also be analogs. It is to Owen's later or 1848 concept that Boyden would have us return.

The concept of analogy, like that of homology, has undergone changes with time. When with the acceptance of the evolution doctrine the basic significance of homology became that of agreement in origin and descent, the concept of analogy, by dictates of contrast, came generally to signify, first, a separate, independent origin, and, second, convergent evolution, leading to a like use and to a superficial similarity in structure. The trend of thought has been in that direction, even though a considerable number of biologists, agreeing with Boyden, have stated their belief that analogy should apply to any agreement in general function, whether or not the structures involved are homologous. But even those who accept this broader definition are wont to write such phrases as "analogous only" or "analogous but not homologous," to indicate that they too associate with the term analogy a connotation of independent origin. Dr. Boyden writes that when he took a poll of recent text-book opinion he found that a very large majority of the authors associated independent origin or superficial similarity with analogy. The "last word" (Webster's New International Dictionary of the English Langauge, second edition) gives the biological definition of analogy as "correspondence in function between organs or parts of different structure and origin;—distinguished from *homology.*" This dictionary definition does not interpret all usage, but it seems to reflect the opinion of the majority of present-day biologists.

Analogy, like homology, should apply to both functions and structures. As Tait pointed out, analogy was originally a term applicable to structures. Many biologists, however, would treat it as essentially pertaining to functions. But structures and functions exist together as inseparable manifestations, as we noted in applying the

homology concept to both. Since homology expresses the relation between characters, whether of function or structure, that are fundamentally alike and of common origin, the contrasting term, analogy, should apply to either functions or structures, when these are only superficially alike and are not monophyletic.

Ordinarily, in testing the phyletic significance of a character, the biologist will contrast homology and analogy. But when a broader antonym is needed, without restriction as to agreement in function or superficial similarity, the character involved may be denoted as nonhomologous (or as polyphyletic, polygenetic or heterophyletic). When the whole emphasis is on community of origin, such terms as monophyletic, monogenetic and homophylic are available. The term "analogous" is now properly applied, I think, only to structures and functions which serve the same use, but which are of independent origin and history. There seems to be no need for a return to an older concept of either analogy or homology.

SUMMARY

Boyden urges that we return to Owen's original, century-old definitions of homology and analogy—analogy to signify a similarity of structures in use, without regard to fundamental agreement in structure or evolution; that is, without regard to homology; and homology to indicate a basic agreement in structure and relative position, without regard to functional similitude.

But the concept of homology has evolved through the century, particularly under the influence of the doctrine of evolution. Homology has come to signify an agreement in evolutionary derivation and in embryonic development.

The traditional and persistent limitation of the homology concept to structures has overemphasized morphology and is inconsistent with the modern view that structures and functions are inseparably associated. It is desirable that the term homology be regarded as applicable also to intrinsic functional mechanisms, reflexes,

behavior patterns and other functional attributes, when they indicate a common heritage.

Attempts to dissociate "serial homologies" from "true or special homologies," and various proposals to break down homology into a series of relations each with a separate name, have largely been abortive and are not regarded as wise. A consideration of homologies between diffuse elements helps to clarify the general picture. Endless inconsistencies would arise from the application of suggested restrictions of the homology concept.

Homologous relationships are very complex. There are many degrees of specificity in homology. Two characters may be homologous from one point of view but not so from another. Where to draw the line is a function of the special needs in any comparative study. Many complexities in homological relations come to mind when we review the facts of anatomy, variation, genetics and experimental embryology, and the uncertainties may be accentuated in studying closely related kinds of animals. Such irregularities encumber almost all biological concepts, but destroy neither their validity nor their usefulness.

What may be called independent homologies—more or less identical but independent modifications of homologous structures or functions, agreeing with typical homologies in all respects other than time of origin—provide a troublesome transition between homologies and analogies. There are genetic discontinuities of various kinds and degrees in the lineage of characters.

A modern concept of analogy is that of the agreement in use of characters (structures or functions), which have had a distinct evolutionary origin. There seems to be no special need for a return to a century-old concept of either analogy or homology.

Both concepts—of homology and of analogy—should be recognized as involving grave complexities. These ideas involve the same sort of inexactitude that is inherent in such principles as those expressed in Haeckel's biogenetic

law and Dollo's law of irreversible evolution. Precision in any of these concepts should not be allowed to transcend the complexities that exist. Despite these difficulties, the concepts of homology and analogy retain, in their evolved, modern meaning, a place of importance and value in biology.

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DISTRIBUTION AND VARIATION IN POCKET GOPHERS, *THOMOMYS TALPOIDES*, IN THE STATE OF WASHINGTON

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INTRODUCTION

FROM an evolutionary standpoint the pocket gophers of the genus *Thomomys* comprise one of the most plastic groups of North American mammals. Their range of variation in morphological characters is extreme. In color they vary from nearly white in some desert species to almost black in others. In the skull, variations in ridging, size, proportion and in shape of the cranial bones, are clearly exhibited. The habits of pocket gophers are such that relatively minor topographic or environmental barriers often effectually limit their areal distribution, although the same barriers may have little or no effect on other vertebrates. These conditions have contributed to the formation of a large number of subspecies (geographic races) of pocket gophers in the western United States, each comprising a complex distinguishable by average differences in size, color or cranial characters from its kindred subspecies.

The present report is based on a study of the distribution of mammals in a region of which parts were recently subjected to continental glaciation and of which other parts were strongly affected by the near-by ice. We have attempted to point out the relationships between the present distribution of the pocket gophers of Washington and the probable history of their origin, migration and eventual geographic isolation. We have sought to interpret on a genetic basis, wherever possible, the variation that is now exhibited by these animals.

Our source materials include 710 specimens of gophers collected by us or examined in museums over the past ten

years. Our largest series were taken from the prairies around the south end of Puget Sound, the Puget Sound Trough of geological terminology, in the three winters of 1938–1941. Topotypes of all races of pocket gophers found in Washington and the type specimens of several races were available to us. Body measurements and weights were made in the field by each of us, and cranial measurements were made by one of us (Dalquest) in the laboratory. Specimens used for demonstrating subspecific differences were fully adult but not "very old" animals. We did not have sufficiently large series of individuals of the same age and sex from single localities to compare populations by means of standard errors.

For the use of specimens in their care and valuable assistance in other ways, we are deeply indebted to Dr. H. H. T. Jackson, U. S. Fish and Wildlife Service, Mrs. Martha Flahaut, Washington State Museum, Dr. George E. Hudson, Charles R. Conner Museum, and Dr. E. Raymond Hall of the Museum of Vertebrate Zoology, of the University of California at Berkeley. From the last mentioned the writers acknowledge critical assistance in the preparation of this paper.

Immigrational History of the Pocket Gophers of Washington

The pocket gophers of the state of Washington may be classed for convenience into two groups: a relic group, which occupied the state in preglacial or interglacial times, and a group of immigrants from the south and east which entered the state shortly after the Pleistocene. The earliest described race of the relic group is *douglasii,* and this group is therefore referred to as the *douglasii* group of subspecies. For a similar reason, the immigrants are termed the *fuscus* group.

It is difficult to select morphological characters which will consistently separate the two groups. Generally speaking, the gophers of the *douglasii* group are larger and possess larger, heavier skulls with relatively longer

rostra and more flaring zygomatic arches. Exception must be made for certain races of the *douglasii* group found in the Puget Sound area which do not show all these differences.

The *douglasii* group appears to be more restricted in habitat than the *fuscus* group. The *douglasii* gophers are

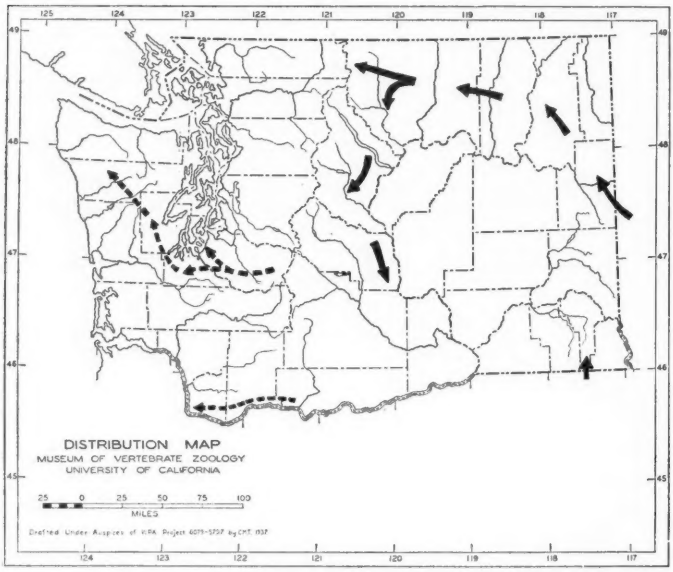

FIG. 1. Postglacial movements of the two principal stocks of gophers in Washington. At the climax of the Pleistocene only gophers of the *douglasii* group remained in the state and these were confined to the southern Cascade Range and the Columbian Plateau of southeastern Washington. From the Cascades, gophers spread westward (broken arrows) to portions of the Puget Sound Trough and the Olympic Mountains; in southeastern Washington they remained to later intergrade with members of the *fuscus* group. With the retreat of the glacial ice, gophers of the *fuscus* group invaded (solid arrows) from Idaho and northern Oregon.

found in the grassy prairie lands of the Palouse country of southeastern Washington, in glacial outwash and river terrace prairies of western Washington, in the open, grassy prairies of the Columbia River Valley of southern Washington, and in the alpine meadows of the Cascade and Olympic mountains. They prefer well-watered,

grassy, prairie lands free of even moderately thick forest or brush. An exception is the desert-inhabiting race, *devexus*.

Gophers of the *fuscus* group, on the contrary, occur in many kinds of habitats. We have found them in baked, desert loess-clay, grasslands, ground moraine, open woods, alpine meadows, and damp, almost marshy lands.

With the exception of *Thomomys talpoides tacomensis*, taken on agricultural land, we have found the *douglasii* gophers only in relatively large colonies. Most of the colonies included from fifty to several thousand individuals living in close proximity to each other. Even near the main colonies, small areas of land capable of supporting from one to ten gophers almost always are unoccupied.

Gophers of the *fuscus* group may be abundant in, and occupy all of, a suitable area, but seem not to live as close to each other as do individuals of the *douglasii* group. It is almost the rule, in Washington at least, to find *fuscus* gophers in small groups. This is true even on extensive and uniform terrain which gophers might be expected to occupy *in toto*. The antisocial and independent habits of the *fuscus* gophers and their high degree of tolerance of variations in habitat probably account in part for their success in extending their range at the expense of the earlier established *douglasii* gophers.

Previous to the last Pleistocene glaciation (Wisconsin Glaciation in eastern Washington, Vashon Glaciation in western Washington), pocket gophers of the *douglasii* group apparently occupied all the potential range of the species in the state. This range might have included all of Washington from the Cascade Mountains eastward. The forested areas of western Washington probably never supported gophers.

The descent of the Vashon-Wisconsin ice sheet completely eliminated gophers north of the drift border, in general, the area north of the east-west segment of the Columbia River in northeastern Washington (Flint, 1937, p. 212). Frigid climate prevailing in the Cascade Moun-

tains as far south as Mount Rainier is thought to have exterminated gophers north of this area. The withdrawal of the ice some ten thousand years ago, then, found the *douglasii* gophers restricted to the southern Cascade Mountains, the Columbian Plateau, and southeastern Washington.

The douglasii gophers isolated in the southern Cascade Moutains were extremely plastic, in a systematic sense. Within this area three geographic subspecies occur today: *Thomomys talpoides shawi,* in the Mount Rainier area; *immunis,* in the Mount Adams area; and *limosus,* in the Columbia River Valley. Individuals of the *limosus* stock migrated westward, early in Recent time, along the Columbia River, to certain Pleistocene river terraces in Clark County, where the race *douglasii* is now isolated.

The outwash train by which the *douglasii* gophers reached the Vashon outwash prairies in the Puget Sound area is now overgrown with forest. To the best of our knowledge no gophers now occur in this train. There is an isolated population of the race *yelmensis* at Vail, Thurston County, and a distinct race (*glacialis*) near Roy, Pierce County, north of the Nisqually River and north of the population on the prairie at Vail. Outwash prairies, free of gophers but possessing Mima mounds (unique structures formed by pocket gophers; Dalquest and Scheffer, 1942), connect the gophers at Roy with those of a similar but distinct race, *tacomensis,* found near Steilacoom, Pierce County.

Outwash prairies, some of which bear Mima mounds, connect the population at Vail with another population of the race *yelmensis* near Tenino, Thurston County. *T. t. tumuli* occurs in Thurston County north of the range of *yelmensis.* Near Olympia, Thurston County, another distinct race, *pugetensis,* is found. West of Tenino, near Rochester, Thurston County, is another isolated population of *yelmensis.*

Mima mounds west of Rochester, in the Chehalis River Valley near Satsop, indicate that gophers migrated along

this route to reach the outwash prairies on the southeastern base of the Olympic Mountains where the race *couchi* is now isolated on prairies near Satsop, and Shelton, Mason County (see Fig. 2). Gophers from these prairies probably moved up into the alpine meadows of the Olympics, where the race *melanops* is now found.

The *douglasii* group of gophers probably once extended in a continuous or nearly continuous band from Mount

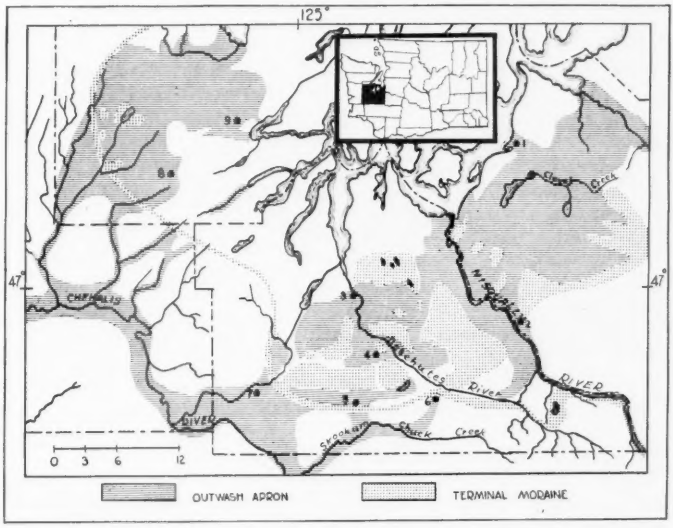

FIG. 2. Distribution of gophers in the Puget Sound area with relation to the Vashon outwash apron.

Rainier around the southern end of Puget Sound to the Olympic Mountains, on the glacial outwash prairies. The prairies consist of a deep bed of coarse gravel underlying a thin bed of silt-gravel. The coarse gravel causes rapid drainage of rainfall. In summer the soil on the prairies dries out so thoroughly as to kill seedling trees before they become established, and this permits the prairies to exist. They are semidesert areas surrounded by dense forests.

The *douglasii* pocket gophers seem unable to exist in

forested areas, even on the outwash prairies. Only the subspecies *tacomensis* occurs on cultivated land, away from outwash prairie. With this exception, non-prairie areas or forested areas on the prairies serve as effective barriers to gophers. The once continuous band of outwash prairie extending around southern Puget Sound is now broken up by forests into numerous small prairies, resulting in the isolation responsible for the numerous subspecies of gophers in the Puget Sound area. Many former prairies which are now completely forested, bear remains of Mima mounds showing that gophers lived there in the past. At least one large prairie and two small ones, free of forest, possess Mima mounds, but no gophers now live there. The forest is invading all the prairies now supporting gophers; the area of some of these prairies has been reduced to less than a square mile. On Lost Lake Prairie, Mason County, we caught seven gophers, seemingly the entire population. The gophers of the Puget Sound area are doomed to extinction, perhaps within a century.

On the Columbian Plateau of central-eastern Washington there is a subspecies (*devexus*) of the *douglasii* group that was possibly distinct from the remainder of the *douglasii* group early in post-Pleistocene times. It is a small, pale race, seemingly well adapted to the desert region it occupies. This race has the flaring, angular zygomatic arches of the *douglasii* group, and intergrades evenly with *limosus* and *columbianus,* kindred members of the group. Intergrades between *devexus* and members of the *fuscus* group, on the other hand, show dominance of the color factors of one subspecies or the other in that heterozygous individuals have the color of one race or the other rather than being intermediate in color. Some intergrades between *devexus* and members of the *fuscus* group show the color of both parent races on the body of one individual. This condition, seemingly a case of reversal of dominance caused by environmental conditions at the time of moult, is discussed in detail later.

Although *devexus* belongs to the *douglasii* group, it is much different in skull and color from other members of that group. Therefore, and because it has an extensive geographic range, *devexus* is judged to have been isolated from other members of the group for a considerable time. The Columbia River on the north and west and the absence of desert conditions to the north, east and west doubtless confined it in these directions. A barrier does not exist to the south of the range of *devexus* at the present time. The past existence of a barrier to desert forms is indicated not only by the restricted range of *devexus* but by the close relationship of a number of mammals in southeastern Washington to those of the Simcoe Mountain Range of the southern Cascades. The barrier referred to, we have named the Simcoe Bridge. It is conceived of as consisting of the Simcoe Anticline, a high ridge which reaches from the southern Cascades to the Columbia River Water Gap, near Wallula, and this bridge continues on east of there, in the Bunchgrass Hills. A century ago this bridge was an area of bunch-grass, but most of the grass has since been supplanted, largely by sagebrush. When the Wisconsin ice was at its maximum extent, the Simcoe Bridge presumably had a cooler and more humid climate than now. This climate allowed dark-colored, *limosus*-like pocket gophers of the *douglasii* group to live in a grassy area, somewhat resembling an alpine meadow, that stretched from the Cascades to southeastern Washington. Many of the tributaries of the Columbia River lie to the north of the border of the Wisconsin drift. These probably held little or no water while the ice sheet was in place. Therefore the volume of water in the Columbia may have been much less than now and the river less of a barrier to mammals. The Columbia has frozen over in historic times, and the black-tailed jack rabbit is known to have extended its range in Washington by crossing on the ice (Couch, 1927). Presumably the river froze over more regularly in Wisconsin and early Recent times, and pocket gophers might have crossed the

river through burrows in snow covering the ice (see Davis, 1939, p. 240).

Increasing aridity, following the retreat of the Wisconsin ice, closed the Simcoe Bridge to the dark-colored gophers. This same aridity, in conjunction with a cover of sandy, glacial outwash allowed the pale *devexus*, hitherto confined to the Columbian Plateau, to extend its range southward along the Columbia River Valley. The area occupied was only the narrow, desert-like valley of the Columbia itself. The excessive grayness of the gophers found near the Columbia River in Walla Walla, Benton and Yakima counties may represent the influence of this minor movement.

The race *columbianus*, from Walla Walla County, is essentially a population of intergrades between *devexus* and *acqualidens*, but with certain distinctive features of color, size and skull.

The withdrawal of the Wisconsin ice from northeastern Washington freed the land north of the terminal moraine for occupation by gophers. Gophers invaded the area from the east. These gophers exhibit no characters different enough from those of the race *fuscus* to warrant recognition of them as a separate race. Apparently the ground moraine and glacial drift topography exposed by the withdrawal of the ice was so homogeneous that no differentiation took place in the westward migration of the gophers across northern Washington. The race *fuscus* moved southward along the Cascades until it crossed the Wenatchee Mountains and occupied the Yakima Valley to the mouth of the Yakima River.

Another race (*wallowa*) of the *fuscus* group moved northward in the Blue Mountains of northeastern Oregon into the Blue Mountains of extreme southeastern Washington, where it intergraded with *aequalidens*, of the *douglasii* group. The gophers of the higher parts of the Blue Mountains are actually intergrades between *wallowa* and the *douglasii* gophers to the north, but are referable to *wallowa* (see systematic account). These immigra-

tions of *fuscus* gophers almost completely surrounded the *douglasii* gophers on the Columbian Plateau of southeastern Washington (Fig. 1).

Habits of Pocket Gophers with Relation to Speciation

The general habits of pocket gophers have been described in detail by many authors (Bailey, 1915; Scheffer, 1931). We should like to call attention, however, to certain habits that have played an outstanding role in the evolution of the subspecies studied by us. (1) Pocket gophers are almost completely fossorial, rarely appearing on the surface of the ground. (2) They seem to be solitary and, although tending to live in communities, have no social organization; intermingling of the sexes takes place only during the breeding season (Scheffer, 1931). (3) They live in meadows or grasslands; forest or brush serves as an effective barrier to their movements. (4) They eat or otherwise destroy the roots, stems and leaves of plants; but we judge that, in the majority of cases, the burrowing and mounding habits of gophers stimulate plant growth, by loosening the soil, to a degree that compensates for the destruction of vegetation within the home territory of any individual (Dalquest and Scheffer, 1942). This natural balance allows a suitable habitat to be indefinitely occupied by gophers without depletion of the food supply, provided, of course, that disruptive changes in the environment are not created by outside forces. (5) Gophers tend to remain within a relatively small territory throughout their life.

Climatic, topographic and edaphic conditions in the state of Washington are such that habitats suitable for gophers occur as numerous small "islands" surrounded by uninhabitable territory. The total population of gophers within the range of any described race may number many thousands. The range of a race is not continuous but is made up of countless independent "sub-populations" including tens, hundreds or thousands of animals.

The effect of this isolation of individual units within a larger taxonomic group is pronounced. Mutations appearing in a small, isolated population may be lost, may be retained in a certain proportion of the population or may become fixed and probably homozygous for the entire population, in some populations seemingly without the operation of natural selection. The smaller the population, the more rapidly a factor becomes lost or fixed (Dobzhansky, 1937, p. 182). A race of pocket gopher, then, may be regarded as a group of populations, in each of which the trend of variation is along independent lines. For example, if one were to arrange graphically on a distribution curve the measurements of a single bone in all members of a subspecies of gopher, the curve would exhibit minor nodes, corresponding to the sub-populations, along its length.

The geographic races of pocket gophers in Washington are isolated from each other by topographic and ecologic barriers, such as rivers and mountain ranges, which are of a relatively stable and permanent nature. The barriers isolating sub-populations within a race, forests, for example, are temporary and, although they may stand for years or even centuries, they can be expected eventually to break down and permit intermingling of sub-populations.

Microgeographic races within the range of a subspecies are familiar to all students of *Thomomys*. For the most part these morphologically differentiated populations are separated only by average differences that may represent minor mutations in the multiple factor series for size or color. A striking mutation in a population from Glacier Basin, Mount Rainier National Park, is shown by three or four specimens which represent two generations. They have an extra cranial bone, a small "internasal," situated between the nasals and the frontals (Fig. 3). Probably the bone has no selective value, and may even be a hindrance to the individual which possesses it. The factor or factors for this bone seem to be fluctuating by chance in a small population, and may later become fixed or lost.

The independent evolution of isolated populations within the range of a subspecies and the subsequent intermingling of these populations through the removal of temporary natural barriers, represent diametrically op-

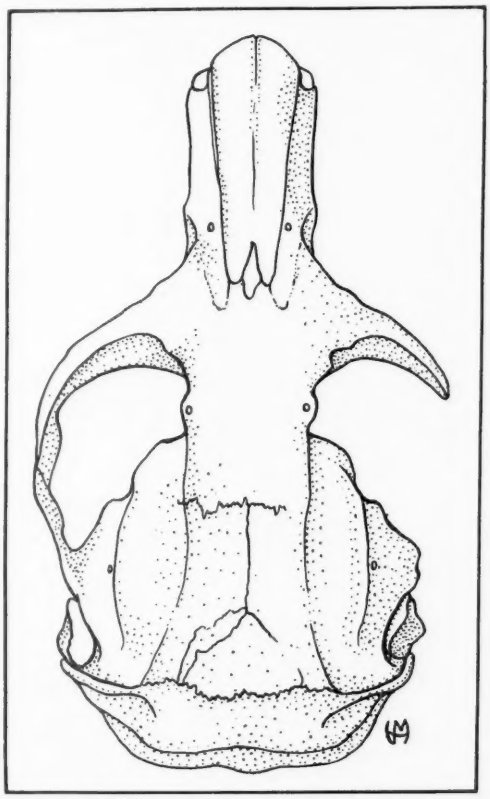

FIG. 3. A cranial mutation in *Thomomys talpoides shawi*. Three of four specimens from an isolated glacial circue on Mount Rainier, Pierce County, possess this "internasal bone." The bone is present in at least two different generations. 3 × natural size.

posed processes. The first tends to establish relatively homozygous entities, whereas the second tends to destroy them.

Evolution of the geographic race as a whole may be in-

fluenced in two ways as a result of these processes. The mingling of a population relatively homozygous for a mutation with a population lacking the same mutation might result in the gene again fluctuating in frequency in each generation in the combined populations. The gene might thereby eventually become either lost or fixed. A mutation might, through a series of "conquests," be spread throughout the geographic race, and with each conquest its chances of ultimate survival would be increased. Such a hypothesis accounts for the differences between the numerous geographic races of pocket gophers, as well as for the countless differentiated populations of less than subspecific rank.

Secondly, microgeographic isolation of small populations would provide reservoirs of differences upon which natural selection might act. A mutation of slight selective value is likely to be lost in a large population, on the basis of chance alone. But if the mutation is homozygous throughout a small population, which mingles with other populations at a later date, its chances for survival might be markedly increased because of its selective value. Microgeographic races might also give a population of gophers an added advantage in meeting such changing environmental conditions as followed the retreat of the continental glaciers from the state of Washington.

Broadly speaking, the differences separating any population of gophers from surrounding populations might have been derived in at least two ways: (1) from mutations which became homozygous for the whole population or which are still fluctuating, that is, which are phenotypically expressed in a certain proportion of the population; (2) by the loss of certain allelomorphs in an isolated population derived from a population in which certain factors were fluctuating, while in the other, original, population these factors might have become fixed. Nearly all microgeographic variations represent slight average differences in size or proportion of body, color of pelage or size or proportion of cranial bones. We feel that most

differences are the result of slight changes in multiple factor series. Some changes in cranial bones may represent single factor mutations.

Size and cranial aberrations or anomalies of a quantitative nature, resulting from genetic changes, are difficult to separate from non-genetic variants of the usual modification curve. One cranial aberration, that of the "internasal" bone, has already been discussed.

Quantitative aberrations in color are more easily detected. A number of these have been found in gophers in Washington. The most striking is the absence of the proximal color band of the fur. "Recessive spotting" is the commonest type of color aberration found by us. Gophers with recessive spotting are flecked dorsally or ventrally with small, irregular, white spots. The spots may vary in number from one to a dozen on an animal and are largest and most numerous on the ventral surface.

One gopher from Mount Adams, Klickitat County, is blotched with white on the ventral side and possesses a white line on the head, extending from the nose, posteriorly between the eyes to the forehead. Whether this specimen represents an extreme case of recessive spotting or involves another type of mutation can not be determined.

Problems of Variation in Races of Pocket Gophers from the Puget Sound Area

Although the entire state of Washington is included within the scope of our investigation we have studied with the greatest intensity the variation among gophers of the prairies of the Puget Sound area. Here six races are concentrated in a relatively small area where the environmental factors that might have contributed to their speciation are more plainly evident than in the parts of eastern Washington which are occupied by gophers.

In 1899 Merriam named *Thomomys douglasi yelmensis,* the first subspecies of gopher to be recognized from

the Puget Sound area. Twenty years later Taylor (1919) named a second subspecies, *tacomensis,* from a locality thirty-five miles northwest of the type locality of *yelmensis.* At that time he remarked: "The pocket gophers of the isolated prairies of western Washington show the effects of segregation. Broadly speaking, one may say that those inhabiting each prairie represent a local variant. While the characterization of each of these would be confusing, the recognition of the more obvious forms is desirable. *Thomomys douglasii douglasii* is one of these, *T. d. yelmensis* another, and *T. d. tacomensis* a third." Although the differences separating the isolated populations of gophers in the Puget Sound area were recognized at that time, it was not until twenty years later that the subject was reexamined by Goldman (1939) and Dalquest and Scheffer (1942).

Certain factors appear to have been more significant than others in the evolution of the gophers of the Puget Sound area. The time element, or period of isolation, is relatively short and is thought to have been of approximately the same duration for all of the described races. As previously stated, the ancestors of the Puget Sound gophers moved down the narrow Nisqually Valley from Mount Rainier as a homogeneous stock. We conceive of this migration as the cumulative seasonal progression westward of young gophers toward the attractive but unoccupied area, rather than as the pioneering advances over long distances by adult animals. The actual advance of any one gopher in its lifetime may have been but a few hundred feet. After the formation of the Vashon Puget outwash aprons, ten to twenty thousand years ago, additional time was required for the development there of vegetation capable of sustaining gophers, and then for the invasion of the aprons by gophers. About ten thousand years would represent the maximum length of time that any population of Puget Sound gophers has been isolated.

Mineralogically, the rock materials composing the

Puget Sound prairies are alike. All were formed of glacial drift reworked and redeposited by water.

The prairies occupied by gophers lie at nearly the same distance above sea level, between tidewater and an elevation of 500 feet.

Records of the United States Weather Bureau show that the yearly variations in temperature and precipitation on any prairie exceed the variations among the different prairies in any one year, and as a consequence the climate may be considered uniform over all the prairies.

Although the individual prairies are identical in the above-named ecologic features, they do exhibit striking differences in depth of soil, size of soil particles and vegetative cover—all closely related attributes. Outwash prairies consist of a deep layer of coarsely stratified yellow gravel of unknown thickness containing little interstitial sand or silt and a layer of topsoil of black silt-gravel. We suppose that the outwash aprons originally consisted of a layer of stratified gravel covered with a layer of flood-plain silt. The activities of plants and animals, especially of moles (*Scapanus*) and pocket gophers, have thoroughly mixed a part of the stratified gravel with the silt, forming the topsoil. The quantity of gravel mixed into the layer of silt determines the stoniness of the soil on the prairies. Where the original layer of silt was deep, as on Bush Prairie (in this case more than five feet), the ordinary burrowing activities of animals did not extend down to the surface of the gravel and, as a consequence, the soil there is almost pure silt. On Scotts Prairie the layer of silt was, originally, only a few inches thick, and the present soil is extremely stony. On every prairie in the vicinity of Puget Sound the stoniness of the soil is inversely correlated with the depth of the soil.

On all but the deep-soiled Bush and Roy prairies, pocket gophers have accumulated great masses of soil, known as Mima mounds. The complicated formation of these mounds has been discussed in detail by Dalquest and Scheffer, *loc. cit.* Mima mounds resemble great spheres,

partially buried in the earth. On many prairies these mounds are now the only places occupied by gophers.

Differences in vegetation on the prairies inhabited by gophers are difficult to measure at the present time. Grazing by sheep and cattle and the introduction of weed plants have radically changed the composition of the vegetation on most of the prairies, so that any qualitative differences in vegetation which once might have existed

FIG. 4. A prairie inhabited by gophers in the Puget Sound area. Scotts Prairie in Mason County is one of the native grasslands that dot the timbered coastal region. These consist of deep beds of coarse gravel covered by soil layers of porous silt or silt-gravel. The soil layers become too dry in mid-summer to support the growth of seedling trees. Scotts Prairie is the type locality of *Thomomys talpoides couchi*.

among them can no longer be seen. Considering the nearness of the prairies to each other and the similarity of many of the environmental factors, it is likely that any original qualitative differences in vegetative cover were slight. Quantitatively there are noteworthy differences; the deep-soiled prairies bear a lush vegetation of grasses and annuals, whereas the thin-soiled prairies bear a sparse cover consisting mainly of mosses and lichens.

Three important, measurable differences in these prairies, namely, depth of soil, size of stones or smaller inclusions in the soil and vegetation, thus result from a single factor—the difference in the depth of the layer of soil. If any or all of these differences has acted as a selective factor in the evolution of the gophers, variation in the populations should be correlated with depth of soil on the prairies. In an effort to determine this we have collected series of study specimens of pocket gophers and for each prairie have recorded the edaphic and vegetative conditions.

Description of the Prairies Inhabited by Gophers in the Puget Sound Area

The following brief descriptions of the Puget Sound gopher prairies are arranged (with the exception of that of the Steilacoom Delta) in order of decreasing depth of soil, or, in the case of prairies which have Mima mounds, in order of decreasing height of the mounds.

1. *Bush Prairie,* 4 mi. S Olympia, Thurston County (type locality of *pugetensis*), includes the Olympia airport and fields to the west of the airport. The soil here is more than 5 feet deep, soft and free of pebbles; no Mima mounds are present; vegetation is high and rich on areas ungrazed by cattle.

2. *Roy Prairie,* 2 mi. S Roy, Pierce County (type locality of *glacialis*), has an area of deep soil, about 4 feet thick, where gophers occur, just below and south of a Pleistocene terrace on the north border of the prairie. The soil resembles that of Bush Prairie, but is shallower and has a few pebbles. Vegetation is high and lush. One mile south of the deep-soiled area the soil becomes thin and the prairie is studded with kettles and Ford mounds. A few Mima mounds occur at the northern edge of the shallow-soiled area, and less than a dozen old gopher workings were discovered there.

3. *Rocky Prairie,* 5 mi. N Tenino, Thurston County (type locality of *tumuli*), is extensive and has the largest

Mima mounds now inhabited by pocket gophers in the Puget Sound area. The soil is stony, but in some places 4 feet deep. Vegetation on the mounds is dense, but it is scant or absent in the areas between the mounds.

4. *Rochester Prairie,* 2 mi. N Rochester, Thurston County (in range of *yelmensis*), has become separated from Grand Mound Prairie in relatively recent times. The Mima mounds are smaller than those on Rocky Prairie. The soil is stonier than that of Rocky Prairie, but the vegetation of the mounds is as dense, although where the gophers live the soil averages only about 3 feet deep.

5. *Grand Mound Prairie,* 2 mi. S Tenino, Thurston County (type locality of *yelmensis*), closely resembles Rochester Prairie, but the Mima mounds are slightly smaller. The stony soil, of about the same depth, and the amount of vegetation on the Mima mounds of these two prairies seem alike.

6. *Vail Prairie,* 1 mi. W Vail, Thurston County (in range of *yelmensis*), has soil rather shallow, averaging 3 feet or less in depth where the gophers live, and stonier than that of Grand Mound Prairie. No uncultivated or ungrazed land remains on the prairie, and its vegetative cover now is not comparable with that of other prairies. The remains of Mima mounds, nearly eradicated by cultivation, are smaller in diameter than the mounds of Grand Mound Prairie.

7. *Lost Lake Prairie,* 15 mi. NNE Satsop, Mason County (in range of *couchi*), has been nearly eliminated by forest. The soil is thin, not more than one foot deep, and rocky; the vegetation is sparse. Mima mounds are low and poorly developed. Less than a dozen gophers are thought to exist here.

8. *Scotts Prairie,* 4 mi. N Shelton, Mason County (type locality of *couchi*), is rather small (Fig. 3). The soil is only about 9 inches thick and is stony; the vegetation is scant. Mima mounds here are the smallest known to us, being less than 2 feet high.

9. *The Steilacoom Delta,* 2 mi. NW Steilacoom, Pierce County (possibly the type locality of *tacomensis;* certainly within a few miles of the type locality). Here pocket gophers occur on the topset beds of a great delta built into the Pleistocene Lake Russell (Bretz, 1913, p. 137). The soil layer here lacks the distinct vertical stratification typical of the outwash prairies. Gophers are almost absent from adjacent outwash prairies and are now restricted to non-prairie agricultural lands on the delta where the soil is reddish sandy-gravel. Pocket gophers could not have lived in the timber of the delta before it was cleared for agriculture. They must have lived on some of the outwash prairies to the eastward and later invaded the delta. A few gopher workings and some low Mima mounds were found on prairies which grade gradually into the red-soiled topset beds of the delta.

Variations in Size of Gophers from the Puget Sound Area

Five races of gophers, living on eight separated prairies in the Puget Sound Trough, may be divided into three size groups: (1) In the group of largest size, three races are included. Two are from the deep-soiled prairies (*glacialis* and *pugetensis*) and the other from Rocky Prairie (*tumuli*) where the Mima mounds are large. (2) On the three prairies where the Mima mounds are of medium size, the gophers (*yelmensis*) are also of medium size. (3) The smallest race of gopher found in the Puget Sound area (*couchi*) lives on Lost Lake Prairie and Scotts Prairie, where the soil is thinnest.

A sixth race of gopher (*tacomensis*) from the Puget Sound area lives in a habitat different from that of the other five. The soil conditions in its habitat are not comparable to those on the outwash prairies, where the lower limit of the soil layer is fixed by a "floor," or layer of stratified gravel. The habitat suitable for gophers includes only the soil layer above this floor. The sixth race lives in the reddish, sandy-gravel that constitutes the soil

of the Steilacoom Delta. This delta lacks the restricting floor of pure gravel, and the vertical limits of the activities of gophers are regulated only by the whims of the individual. Thus, whereas the maximum depth of gopher habitat on the outwash prairies can be judged with accuracy, no accurate prediction can be made for the gophers living on the Steilacoom Delta. About all that can be said is that gophers would be expected to be of large size, as they are.

TABLE I

CORRELATION OF DEPTH OF SOIL (OR HEIGHT OF MIMA MOUNDS) WITH SIZE OF ADULT MALE POCKET GOPHERS IN THE PUGET SOUND AREA

Name of prairie	Specimens	Soil depth*	Total length	Weight
		ft.	*mm.*	*gm.*
Bush	14	5	223	123
Roy	20	4	225	128
Rocky	11	4	225	140
Rochester	16	3	215	117
Grand Mound	21	3	213	121
Vail	12	3	216	126
Lost Lake**	..	1	...	...
Scotts	13	¾	196	87

* Generalized depth where pocket gophers are living most abundantly.
** Only female gophers taken on Lost Lake Prairie. For comparison see Table III.

It is concluded that the size of the pocket gophers of the outwash prairies is positively correlated with depth of soil. This agrees with the conclusion arrived at by Davis (1938).

Having shown that size of pocket gophers is directly correlated with depth of the silt-gravel layer on the outwash prairies occupied and having presented evidence that populations about Puget Sound originated from a common stock and therefore had identical or nearly identical gene compliments, we deduce that depth of soil, or some function therefore, has acted as a selective factor to limit the size of the gophers.

As to selection, there are two possible methods by which it might have been brought into play. In each population, new factors for size might have appeared. The size most favorable for the depth of soil of the habitat occupied may have been retained through selection. Serious objections to this view are: (1) the small size of the popu-

lations (larger in the past, it is true, but still small as compared to other species of rodents), which would tend to limit the appearance of new factors; and (2) the relatively short period of isolation (less than ten thousand generations), which we feel would scarcely allow for the origin and spread of the necessarily large number of mutations and the subsequent elimination of all but the most favorable. It seems improbable that each of the six races had a favorable mutation soon after it was isolated.

We are inclined to a second view, namely, that in the original population occupying the outwash aprons, size was variable and was controlled by a number of pairs of alleles in a multiple factor series. Under isolation and the restricted environment of the silt-gravel layers on the prairies, individuals with factors for a size most efficient for their particular environment were favored by selection, until the entire population became relatively homozygous.

There is thus no necessity for assuming that new factors for size appeared, but only that there was a loss of one or more alleles and that there occurred a fixation of factors already present. Newly acquired factors may, it is true, have contributed to the end result. Hagedoorn and Hagedoorn (1921) show that the smaller a population (and ours are small), the more rapidly a factor becomes fixed or lost, owing entirely to the operation of the laws of chance.

In addition to absolute size of body and skull, the relative size of parts should be mentioned. In general there is a strong, positive correlation between size of body and size of skull. In specimens of *yelmensis* examined the correlation between condylobasal length and total length of body had a Piersonian coefficient of 0.61. In *pugetensis* the coefficient of correlation between body length and weight was found to be .68. The relative sizes of the various parts of the skull vary considerably between races and are generally reflected in the standard measurements taken. A slightly larger body in one race than in another

is accompanied by a much larger skull and on the larger skull, in response to larger muscles, there are strong ridges, crests and tuberosities which are only faintly indicated or absent on the skulls of races with smaller bodies.

The foregoing quantitative characters are all expressions of size and are phenotypic expressions of the genes controlling size. Sumner (1930) found size in *Peromyscus* to be explained best by the multiple factor hypothesis and this hypothesis probably applies also to the pocket gophers.

VARIATIONS IN COLOR OF GOPHERS IN THE PUGET SOUND AREA

All prairies inhabited by pocket gophers in the Puget Sound area lie within the Humid Transition Life-zone. Subspecies of birds and mammals from within this life-zone are, with few exceptions, darker or more "saturated" than subspecies from inland areas to the east. This is true of pocket gophers in Oregon and California, but not in the Puget Sound area. Subspecies of gophers around Puget Sound vary considerably in color, but all are lighter than some of the darker subspecies from east of the Cascade Mountains, although some races from the latter region are lighter than those of the Puget Sound area. It should be noted here that one post-Pleistocene emigrant race of the *douglasii* group, *aequalidens,* in southeastern Washington retains its dark color, although surrounded by pale races.

No correlation was found between the color of pocket gophers from the various prairies around Puget Sound and any observable factor in their environments. Certainly color is not correlated with depth of soil. This lack of correlation in color of gophers on the outwash prairies, where differences in habitats are easily observed, leads us to think that there is no strong selective factor for color operating on the races of the Puget Sound area. In these same populations, where depth of soil has acted

to determine the mean size of the pocket gophers, color factors seem to have become lost or fixed irrespective of any discernible selective factors. It seems improbable that the gophers of the Puget Sound area have been immune to the influence which operates in the humid coastal area to produce dark color in most vertebrates. We conclude that depth of soil, in a relatively short time of isolation, is a much more powerful selective factor for size than is any discernible selective factor for color. Probably factors, of the environment, selective for color are present, but their effect is so slight as not to overcome the fixation resulting from chance combinations of alleles of a multiple factor series. If different alleles have become lost or completely fixed on each prairie, this would account for the variations in color from prairie to prairie and the almost complete lack of overlapping of color in the several races.

Qualitative Differences in Gophers of the Puget Sound Area

Two examples of variation of a qualitative nature have come to our attention. One, the presence of an extra cranial bone, the "internasal," has previously been discussed (p. 318). This bone was found in one old adult and two younger animals, suggesting that a spontaneous mutation arose and persisted over at least two generations. A character of no selective value arising in such a way in a population of gophers might, in a few hundred generations, become homozygous for the entire population. We think that the internasal bone and at least some of the lesser cranial characters such as processes, prominences and angularities found among gophers are single factor characters and as such are fluctuating more rapidly than multiple factor characters. Sumner (1934, p. 145) emphasizes the fact that in the deer mouse, *Peromyscus,* specific differences studied by him have all been multiple factor characters. Qualitative morphological characters, such as the processes, prominences and angularities

typical of the skulls of gophers, however, are rare in *Peromyscus.*

Mutations present in only one or two isolated populations cannot be tested for correlation with environmental factors. Some such characters doubtless have selective value, positive or negative. Others, such as the shape of individual bones and position of auditory tubes, can be assumed to have little or no selective value.

A second variation, physiological rather than morphological, was observed in the tolerance of *Thomomys t. tacomensis* for a wide variety of habitats, including sandy-gravelly soil and thicket-covered land, in contrast to the behavior of the other five races of gophers in the Puget Sound area. We have emphasized throughout this report the complete restriction of the gophers of the Puget Sound area, with the exception of the one race, *tacomensis,* to the silt-gravel layer of soil on the outwash prairies and their absence from forested land. Also, each subspecies has rather distinct limits for size of the individual animal as shown by the small coefficients of variability. Nevertheless *Thomomys t. tacomensis* is an exception to the general rule, possibly because this race moved into soils lacking the definite horizontal limits of the silt-gravel layers on the outwash prairies before the modifying genes of the multiple factor series controlling variations in size were lost through natural selection. That the one race retaining a wide range of variability in morphological characters also retains a wide range of tolerance to environmental conditions, a range wide enough to permit it to invade land recently cleared by man, seems to be more than coincidental. Greater variability in size would scarcely account for greater variability in tolerance. We do not maintain that tolerance is, in this case, linked with size, or even that it is inherited in Mendelian fashion. We merely suggest the possibility of Mendelian behavior. It might well be that an original wide range in tolerance present in the gophers directly ancestral to the present races of the Puget Sound area has been lost

to gophers that, for thousands of generations, have lived in the restricted silt-gravel layer of the outwash prairies. A series of genetic factors for range in tolerance might, in small, isolated populations, be reduced to the few factors of selective value necessary for existence in the homogeneous prairie habitat.

The race *tacomensis,* inhabiting a less stable environment than the other Puget Sound gophers, may have retained more modifying factors of the original size-regulating series. The same may be true of a series of multiple factors controlling tolerance. The two need not be linked, but may have responded to the same selective factors.

(*To be continued*)

MATING TYPES IN PARAMECIUM CAUDATUM

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INTRODUCTION

STUDIES of the sex of Protozoa have been undertaken only in recent years. Contributions to this problem are as yet few, of which the majority deals with various species of *Paramecium*.

It was Sonneborn (1937) who first discovered the two mating types in *P. aurelia*. He considered that the macronucleus rather than the micronucleus is differentiated as to sex. Kimball (1937) studied the inheritance of sex in *P. aurelia* and confirmed the results of Sonneborn, *i.e.*, the sex is determined by the macronucleus. Jennings (1938) investigated *P. bursaria* and found nine mating types falling into two independent groups. Tartar and Chen (1940) studied *P. bursaria* and concluded that it is the cytoplasm which is related to sex.

The mating types of *P. caudatum* have been studied by Giese and Arkoosh (1939) and Gilman (1940). The latter author found from nature five noninterbreeding groups of animals, each with two mating types.

The present work was started in May, 1942, using as material *P. caudatum* of Yunnan, China. Some interesting facts, which have not been recorded by the previous workers, have been observed. These are described in the present paper.

MATERIALS AND METHOD

Three lots of *P. caudatum* were collected from different localities: one (MA) from a small lake in Kunming, the second (MB) from a small pond in Sung-Ming about 50 kilometers from Kunming, and the third (MC) from a rice field in Cheng-Kung about 35 kilometers from Kunming. From MA 15 clones (C1–C15), from MB also 15 clones (C16–C30) and from MC 11 clones (C31–C41) were raised. Other clones (1*a*1, etc.) were raised from the

exconjugants of the above clones. All the clones were cultivated in infusion of rice stalks in small finger bowls. The range of room temperature was from 12° C–24° C.

The clones were examined once in a few days in order to see if any endomixis occurred. This examination was made under a compound microscope. The stains used were acetocarmine and methyl green.

Tests for mating types were made as follows: Individuals from two different clones were mixed on a depression slide in a moist chamber. The mixture was examined frequently. If conjugating pairs occurred, these two clones were said to be of different mating types. The time from mixing of two clones to the appearance of conjugating pairs varied with various clones. Some conjugated immediately, while others required two days or more. In order to facilitate the mating reaction, the moist chambers containing the clone mixtures were placed in a dark chamber and were taken out only during examination.

Total-mount slides were made by fixing the animals in hot (60° C) Schaudinn's fluid and staining with iron alum hematoxylin or Feulgen's stain.

Observation of Mating Types

This observation was continued for three months. The forty-one clones (C1–C41) collected from the field may be divided, according to their sex behavior, into three groups (groups 1, 2 and 3; Table II), each comprising two mating types (types I, II, III, IV, V and VI; Table II). No member of one group can react sexually with any member of the other groups. The three groups are thus independent of one another.

Clones from the exconjugants between type I and type II: Sonneborn (1937) discovered in *P. aurelia* that the descendants of the exconjugant may be all of the same sex as the progenitor, or of the opposite sex, or one half of them are of the same sex and the other half of the opposite sex to their progenitor.

To determine the types of descendants from exconjugants, the method employed by previous workers was followed. A single individual of one type was placed with a single individual of the opposite type on a depression slide. After conjugation, the four descendants of the two exconjugants (each of which had divided into two) were cultivated separately and resulted in four clones. The mating type of each of the four new clones was determined by examining its reaction against the two parental types.

The nomenclature used for the exconjugant lines in this investigation is that proposed by Jennings (1938). "To each pair was given a number, and the two members of a pair were called *a* and *b*. From each member two lines of descendants, derived from the first division of the exconjugant, were isolated; these were designated 1 and 2." Thus the pair 8 furnishes the four lines of descendants 8*a*1, 8*a*2, 8*b*1 and 8*b*2.

In most of my experiments, the behavior of clones derived from the descendants of exconjugants agreed with what Sonneborn found. However, some of the experiments on mating type I by type II gave different results. Among the 78 pairs of type I and type II, 75 pairs produced descendants either of type I or of type II, while the remaining three pairs (1st, 18th and 28th) produced descendants which were neither of type I nor of type II.

From these three conjugating pairs, 12 clones could be raised. But unfortunately some of them died and only 7 clones were raised. These surviving clones were 1*a*1, 1*a*2, 1*b*1, 1*b*2, 18*a*1, 18*a*2 and 28*a*1. The reactions of these seven clones against the two parental types and among themselves are shown in Table I, in which + indicates the occurrence of pairing while — indicates that no pairing occurs.

These seven clones were also tested against the four other types in groups 2 and 3. The results were all negative. Thus we may conclude that a fourth indepen-

TABLE I

THE MATING BEHAVIOR OF SEVEN EXTRAORDINARY CLONES RAISED FROM EXCONJUGANTS OF TYPE I BY TYPE II

	I	II	1*a*1	1*a*2	1*b*1	1*b*2	18*a*1	18*a*2	28*a*1
I	–	+	–	–	–	–	–	–	–
II	+	–	–	–	–	–	–	–	–
1*a*1	–	–	–	–	+	+	–	–	–
1*a*2	–	–	–	–	+	+	–	–	–
1*b*1	–	–	+	+	–	–	+	+	+
1*b*2	–	–	+	+	–	–	+	+	+
18*a*1	–	–	–	–	+	+	–	–	–
18*a*2	–	–	–	–	+	+	–	–	–
28*a*1	–	–	–	–	+	+	–	–	–

dent group, also with two opposite mating types has been derived by conjugation between the animals of type I and type II. Thus there are altogether 8 mating types falling into four noninterbreeding groups as shown in Table II.

TABLE II

THE MATING BEHAVIOR OF FOUR INDEPENDENT GROUPS

Source	Group	Type	1		2		3		4	
			I	II	III	IV	V	VI	VII	VIII
From nature	1	I	–	+	–	–	–	–	–	–
		II	+	–	–	–	–	–	–	–
	2	III	–	–	–	+	–	–	–	–
		IV	–	–	+	–	–	–	–	–
	3	V	–	–	–	–	–	+	–	–
		VI	–	–	–	–	+	–	–	–
Artificially raised in laboratory	4	VII	–	–	–	–	–	–	–	+
		VIII	–	–	–	–	–	–	+	–

The distribution of the clones to the groups and types are shown in Table III.

In the progress of these experiments, no endomixis was found with the possible exception of three clones (C1, C7 and C30). The individuals of these clones on the last

TABLE III

DISTRIBUTION OF THE CLONES TO GROUPS AND TYPES

Group	Type	Clones
1	I	C1–C3, C8–C10, C16, C18
	II	C7, C19–C22
2	III	C4, C11–C12, C25–C26, C33, C40–C41
	IV	C24, C27–C29, C39
3	V	C15, C23, C30–C32, C36–C38
	VI	C5–C6, C13–C14, C17, C34–C35
4	VII	1*b*1, 1*b*2
	VIII	1*a*1, 1*a*2, 18*a*1, 18*a*2, 28*a*1

examination stained very faintly in acetocarmine or methyl green and did not show a distinct nucleus. These three clones were then discarded although it was not definitely established whether they were actually in a state of endomixis.

STRUCTURE OF NUCLEUS

Both Feulgen's technique and iron alum hematoxylin were used. The micronucleus stains homogeneously and no distinct chromosomes can be observed. The structure of the macronucleis of all the clones is the same and their sizes are nearly equal.

The structure of the micronucleus shows some variation. In the process of binary fission, the micronucleus is oval-shaped in metaphase. The chromatin material collects in the equatorial region, which stains deeply. The chromosomes are not counted, but their number is not large and they give the same general picture as Penn's figures (Penn, 1937). It may thus be assumed that in this race, the number is the same as given by him (32–38).

In clones C8 and C28, however, the nuclear structure is different from that described above. In C8, the micronucleus is very small and spindle-shaped. It stains very faintly and no distinct chromosomes can be detected in any phase of the binary fission. In C28, on the contrary, the micronucleus is very large and ovoid in shape, with an attenuated end directed toward the indentation of the macronucleus. The chromatin collects at this end, and chromosomes can not be clearly made out.

Thus all the clones except C8 and C28 show uniform structure in the micronucleus. It may be concluded that the structure of the micronucleus gives no indication that it is responsible for sex differentiation.

DISCUSSION

The studies of Jennings (1938) on *P. aurelia* show that there may be many local races differing in mating types and not reacting with races from distant localities. Gil-

man (1941) studied *P. caudatum* and concluded that there was no evidence for the formation of local groups of mating types which would not conjugate with animals from other localities. Materials for the present investigation were taken from three localities. MA and MB are some 50 kilometers apart, and MB and MC are also about 50 kilometers apart. Yet clones from all three localities are represented in types III, V and VI; those from two localities in types I, II and IV. It is evident that in this investigation locality has no effect on the mating reaction of *P. caudatum.*

Working on *P. caudatum,* Gilman (1941) has reported five groups of animals in nature. But in these studies I have found only four groups of which three were collected from the field and the fourth was raised in the laboratory from the descendants of the exconjugants of group 1. The formation of a new group from exconjugants of another has not been previously reported. Only Jennings (1938) has raised two new mating types of *P. bursaria* from the conjugation between two original mating types. But his two new types belong to the same group as their ancestors, while the two new types I raised form a new group different from their ancestors. This can not be due to reversal of sex (Sonneborn, 1937) because no signs of endomixis have been observed.

In *P. aurelia,* the mating reactions are believed to be determined by the macronucleus (Sonneborn, 1937; Kimball, 1937). In *P. bursaria,* Tartar and Chen (1940, 1941) studied the mating reaction of enucleated pieces and concluded that "the cytoplasm alone (in the absence of the nuclei) exhibits the reactivity and diversity of mating type." In *P. caudatum* it is clear that the micronucleus, as far as its structure is concerned, shows no relation to the mating reactions, since the micronucleus in all the clones except two is uniform in structure. The formation of a new group from exconjugants indicates, however, that the exchange of micronuclear material may have an effect on sex differentiation. It is conceivable that this

differentiation may be affected by the interaction of cytoplasm with foreign nuclear material.

CONCLUSION

(1) Mating types are present in the Yunnan race of *Paramecium caudatum*.

(2) Three noninterbreeding groups, each with two opposite mating types, have been identified from the clones collected from the field.

(3) An additional group (group 4), also containing two opposite mating types, has been raised from the descendants of the exconjugants of group 1.

(4) No geographical difference in mating reaction has been found.

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THE ARCHETYPAL POSITION OF AMPHIOXUS AND AMMOCOETES AND THE ROLE OF ENDOCRINES IN CHORDATE EVOLUTION

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I. INTRODUCTION

NUMEROUS and detailed studies on the comparative anatomy and embryology of present-day chordates, together with the evidence obtained from paleontology, have brought into speculative existence an ancestral organism that is useful in understanding the probable phylogeny of modern vertebrate animals. This hypothetical archetype appears to have been compounded out of primitive parts selected from amphioxus, ammocoete (larval lamprey), ostracoderms and various embryos of higher chordate classes. One purpose of the present paper is to reconsider some characters of the hypothetical ancestor as conceived by early investigators with reference to the question—What recent form appears most closely related morphologically?

The principal aim of this review, however, is to consider some aspects of vertebrate phylogeny and ancestry in the light of our present information concerning the profound influence of the hypophysis and the thyroid gland on development. The possible physiologic significance of these organs on vertebrate phylogeny appears to have received very little consideration by modern workers, and of course, such information was not available to the early students who contributed most to our knowledge of primitive forms. A discussion of these physiologic factors will follow a brief survey of interpretations of the archetypal vertebrate based on morphologic data.

General requisites of an archetype: In their classical studies, the early morphologists generally agreed on what

the fundamental requisites of a vertebrate archetype should be. To them, the ancestral form possessed an ideal primitiveness combined with sufficient generalization to permit all known divergences to occur, progressively or retrogressively. The progressive advancements could proceed directly without preliminary alterations of the original and fundamental design.

Despite the circumstance that representatives from most of the invertebrate phyla were described as progenitors of the chordates, remarkably similar opinions were held by students of ancestry concerning the problems of form, segmentation, symmetry, cephalization, the character of the central and peripheral nervous elements, the notochord and pharynx of the common ancestor of the vertebrates. Although the early students agreed on fundamentals, many of the more detailed parts of the archetype have been variously described by different authorities to conform with the requirements of the particular invertebrate considered by them to have been the forerunner of the vertebrates.

None of the several theories on the origin of vertebrates from an invertebrate precursor has received much common or popular acceptance. Possibly as a consequence, modern students have neglected a considerable amount of valid and valuable morphologic data merely because they were used in connection with unacceptable hypotheses of vertebrate ancestry. This appears particularly true with concepts of primitive cephalization and structural organization of the notochord and pharynx. The studies made to test the theories of vertebrate origin, however, have not only given us some of our best coordinated accounts of the structure of many interesting animals but a much better (if somewhat confused) understanding of the fundamental requisites of the primitive chordate ancestor of the true Vertebrata.

Related modern forms: Among modern animals, amphioxus and ammocoetes appear most closely related to an idealistic chordate archetype. Most students equally

familiar with both types, and acquainted with the vertebrates generally, would probably agree that an amphioxus seems the more primitive and an ammocoete the more generalized. In detailed studies of these forms, however, difficulties are immediately encountered in distinguishing between "degenerate specialization" and "true primitiveness." This is particularly true of amphioxus. However, if we are to employ these forms in the proper reconstruction of an acceptable archetype, distinctions of this sort are obviously imperative.

II. Archetypal Characters of Amphioxus

Present accounts: From a review of modern text-books on vertebrate zoology and comparative anatomy one might assume that most modern authors have accepted amphioxus as the ancestral form of the higher vertebrates as set forth particularly by Willey (1894) and without some of his own qualifications of his theory. Relatively few authors attempt to review other theories of origin. The amphioxus hypothesis appears to have been commonly accepted for two reasons: first, the literature on the descriptive morphology of amphioxus is remarkable for its completeness and excellence, and much of the basic literature was well coordinated and made generally available by Willey; second, the amphioxus theory does not go back to the invertebrates for an ancestor and therefore is not so exposed to attack by the critics of the various hypotheses involving invertebrate phylogeny. These hypotheses, however, concern fundamentally different and more difficult basic problems than does that proposed by Willey.

Although amphioxus has been so generally accepted in text-books as the closest living relative of the vertebrate archetype one could readily consider it as a degenerate divergent type from a common chordate ancestor that gave rise to both acraniates and the craniates. This view proposes that the primitive chordate ancestor not only gave rise to the vertebrate archetype but also gave rise

to the small groups of acraniates that did not follow the line of evolution leading to the higher vertebrates. The acraniates in this interpretation, therefore, do not bear a direct ancestral relationship to them. The belief that amphioxus is more degenerate than commonly suspected has been frequently, if not clearly, expressed by several outstanding students of chordate phylogeny, principally by presenting contrary and conflicting evidence regarding its assumed archetypal characters. These contrary evidences have never been well coordinated or publicized. Thus, amphioxus appears to have been over-emphasized by modern authors as a basic ancestral type merely because it clearly possesses primitive characters and structural simplicity. But structural details and organization of the parts presumed to be primitive, and their relation to the whole animal seems to have received inadequate consideration in most of the commonly read accounts of its phylogenetic position and archetypal characters.

Regardless of the difficulties in understanding various hypotheses of vertebrate origin involving invertebrate phylogeny it is surprising that the amphioxus hypothesis has escaped so much valid criticism. The discrepancies in popular accounts are striking in view of the scholarly work on the comparative anatomy of primitive head segments of chordates generally when considered in connection with the excellent specific descriptions of the head of amphioxus. Modern text-books make little or no reference to the many profound studies on primitive head segments. Another puzzling feature that appears to have been given inadequate consideration in text accounts is the highly specialized atrial cavity of amphioxus and its relation to the pharyngeal clefts and gonads, compared with vertebrate conditions. Many other features of amphioxus are distracting in a vertebrate archetype that are scarcely mentioned or insufficiently emphasized by modern authors; examples are: asymmetry of myotomes and spinal nerves; the peculiar histological character of the notochord, its single sheath and the possible signifi-

cance of its cranial extent; the hundred or more pairs of pharyngeal clefts of the adult which form atypically, open atypically, and incidentally produce a disproportionate reduction of the locomotor region. If one removes the atrium (which is not retained in vertebrates) from amphioxus, some of its more pronounced deficiencies in organization and form as a vertebrate archetype become immediately obvious.

A considerable amount of evidence contrary to the usual acceptance of amphioxus as an archetypal form is contributed by William Patten (1912) in his "Evolution of the Vertebrates and their Kin." Gaskell (1908) in his "Origin of the Vertebrates" also discarded the type as an unsuitable connecting link between the non-vertebrates and the vertebrates. In a more recent account of the "Origin of the Vertebrates," Delsman (1922) gave considerable attention to amphioxus as an ancestral type, but he too had much difficulty with it, and when he dealt with the problem of head segments, referred to the burrowing *Lumbricus* in an attempt to establish homologies. Finally, he, in agreement with most previous anatomists, regarded the brain of amphioxus as degenerate and concluded that "the so-called brain vesicle of amphioxus is not homologous to the brain of the true vertebrates (craniota) but only to the epichordal part of the brain of the latter."

This conclusion is in accord, not only with earlier studies which homologized the "first cranial nerve" of amphioxus with the ophthalmic branch of the fifth of vertebrates, but also agrees with researches in comparative embryology. The developing notochord of all vertebrates consistently extends cranially only to a point just behind the hypophysis. In long extinct fossil forms the notochordal elements can also be traced forward only to the pituitary fossa of the basi-sphenoid bone. Thus the typical forebrain is supported mostly by pre-chordal cartilages.

One may attach further significance to the cranial

extent and amount of the embryonic mesochordal tissue that underlies the developing brain by considering the so-called head organizers. According to Huxley and de Beer (1934) in reviewing the original work of Holtfreter (1933) nervous differentiation is induced in axolotls by underlying chordomesoderm. The neural crest is first induced by the prechordal portions of chordomesoderm. If only a narrow portion of the material was present, the overlying cranial neural plate became correspondingly reduced. Not only does the nervous system become reduced in size but develops incompletely and assumes the character of tail neural tube rather than that of a brain. Thus, the lack of pre- and para-chordal cartilages in the head of amphioxus may help explain the condition of the "brain" of amphioxus as resembling a reduced neural tube.

From the evidence of comparative anatomy of cranial nerves, the conclusion must be reached that both fore- and mid-brain in amphioxus is missing. Since none of the "head" of amphioxus is prechordal, the evidence from embryology clearly shows that were these brain parts to form in the characteristic vertebrate manner they would necessarily have to develop mostly as an extension beyond the present cranial limits of the animal. Therefore, it seems incredible that the brain of amphioxus is primitive and could evolve into a brain morphologically comparable with that of lower vertebrates or approach the condition reached in the early development of any true vertebrate.

One other source of evidence may be cited which is in accord with the views of the comparative anatomists and embryologists concerning the degenerate character of the head of amphioxus. That is the evidence provided by fossil forms of the earliest known chordates, the ostracoderms. These forms had well-defined heads and while they may not have antedated possible amphioxus-like animals which were not preserved as fossils, they definitely indicate that the lack of head parts is not necessarily a

primitive character. Gregory (1933) assumed these forms to represent the basic position in his discussion of the essential stages in chordate phylogeny and he completely ignores amphioxus as an ancestral form.

The conditions that originally started amphioxus on its degenerative line of evolution is, of course, subject to more speculation than an account of the probable sequence of events that would follow the loss of the forebrain and hypophysis. Amphioxus-like types must have antedated the earliest chordates of which we have fossil records; *i.e.*, the armored ostracoderms. Whether the amphioxus type once possessed this armor, or never did acquire it, does not seem important here. However, the soft-bodied forms probably began their burrowing habits relatively early in phylogeny, to escape their more formidable relatives. The loss of sense organs may be regarded as being associated with the semi-sedentary habits of the animal in a darkened environment. Degenerative changes of the olfactory and optic structures if sufficiently extended would lead to the obliteration of olfactory lobes, optic thalamus and optic lobes or midbrain of lower vertebrates and thus cut off practically all functional demands of any parts craniad to the hindbrain. The necessity of a pointed and extended notochord would appear more urgent in an animal with the burrowing habits and environment of amphioxus than the presence of pre- and parachordal cartilages and expanded forebrain. The phylogenetically significant point here would appear to be the accompanying loss of the hypophysis, the master regulating mechanism so essential to advancement of vertebrate characters.

III. Endocrine Factors Affecting Amphioxus

In discussing the acraniates, William Patten (1912) appears to have made a profound and prophetic observation: "There is a strong tendency in the entire group toward a retrograde or degenerate development that appears to be due to some prevalent lack of internal con-

ditions or of materials. It makes its appearance during or shortly after the larval stages, cutting down the first promise of a clear-cut, vigorous organology to one that is feeble, blurred or defective in definition; or one in which important parts are lacking." Here, Patten clearly expresses the opinion that physiologic factors in amphioxus (as in other acraniates) are responsible for the peculiar morphology they exhibit as adults and the atypical and devious developmental path they all follow in reaching the so-called adult condition.

In the light of present information on the physiology of the hypophysis and its thyrotrophic function, the statement of Patten might well be expanded to read somewhat as follows: With the absence of the more cranial head parts, including the forebrain and hypophysis, both nervous and chemical directive forces in amphioxus and other acraniates were critically impaired. The preclusion of thyrotrophic properties within the animal has prevented a typical development and differentiation of the thyroid gland. As a result, the thyroid complex (endostyle) followed a degenerate line of evolution and has lost its capacity to produce the hormones necessary for vigorous growth and metamorphic changes leading to an advanced phylogeny. The lack of these internal materials and conditions has resulted in a defective and feeble line of evolution away from the vigorous vertebrate line. Of all the acraniates, amphioxus (Cephalochorda) alone has succeeded in retaining some little resemblance to the vigorous ancestral stock from which they and the higher chordates have come. But none of the acraniates meet the requirements of a vertebrate ancestor. Their degenerate morphology and peculiar developmental history is about what one would expect in view of modern experimental data concerning organizers and the pituitary and thyroid glands.

IV. Ammocoete as an Archetype

The most complete account of the morphology of an ammocoete in English is that of Gaskell (1908). This

account is not coordinated, however, and is used in connection with a theory of vertebrate origin that was subjected to considerable ridicule. Regardless of the use to which the morphologic data was put, it includes a considerable amount of careful and accurate description of ammocoetes, much of which is original. Gaskell was convinced that earlier morphologists were correct in their opinion of its archetypal fitness, but many of his conclusions concerning invertebrate homologs are unacceptable. This is one of the striking examples of how valid data on the ammocoete are commonly unknown and unread because they are associated with an unpopular hypothesis. Almost all modern text-book accounts of ammocoetes are fragmentary and inaccurate apparently because of the uncoordinated and fragmentary character of the literature. In view of the commonly accepted phylogenetic position of the form, it is surprising that more effort has not been made by modern authors to present a more adequate and accurate account of it.

The larval form of all lampreys is known as the "ammocoete" stage because of the early misconception which regarded it as an adult cyclostome, and resulted in its classification as *Ammocoetes branchialis*. An ammocoete is unique in many ways, but the most striking morphologic feature of the animal is the prolonged retention of many structural characters which are present only during the embryologic differentiation of vertebrates generally. The transformation of ammocoetes, therefore, involve what might be looked upon as a long delayed completion of an interrupted embryonic differentiation which had been prematurely overpowered by dominant growth factors.

In comparison with larval forms of other vertebrates (amphibians) the ammocoete occupies a fundamentally different plane of development. Whereas, the definitive histologic pattern of the thyroid and pituitary glands are fairly well established as embryonic features in frog tadpoles, the formation of thyroid follicles and striking

hypophyseal changes are concurrent with general metamorphosis in ammocoetes. This event in lampreys is several (possibly 4 to 7) years post-embryonic. Thus ammocoetes pass through a prolonged pretransformation growth period with partially developed endocrine organs. Other delayed differentiation that is embryologic in other vertebrates concerns "tubular muscle" of the pharynx, migrating germ cells and the retention of a rudimentary eye.

From the standpoint of comparative anatomy, ammocoetes has long been regarded as the modern form standing nearest to an ideal archetype by leading students of vertebrate phylogeny. Although William Patten (1912) put particular emphasis upon ostracoderms, his material did not allow the extended observations as did the more recently discovered fossils which are monographically described by Kiaer (1924) and Stensiö (1927). These show the ostracoderms to be remarkably similar to the ammocoete with the exception of the exoskeletal armor.

Ammocoetes as unarmored ostracoderms: Some archetypal characters of ammocoetes may be better understood by quoting from Gregory (1933) in his review of stages in vertebrate phylogeny. Writing of the ostracoderms described by the Scandinavians, he stated: "Beneath the braincase was a greatly expanded chamber containing the mouth cavity, the gill pouches, the skeletal partitions between the gill-pouches and the ducts leading to and from the gill openings and the exterior. The arrangement is closely paralleled in the larval stage of the existing lampreys. The same is true of the brain and cranial nerves. The neurologists and students of the classical problem of vertebrate head segments had long ago fixed upon the larval stage of the lamprey as standing nearest among existing forms to the archetypal vertebrates. Thanks to the labors of many investigators, we can now affirm that the ostracoderms as a class were the archetypal vertebrates from which were derived, on the one hand, the so-called jawless cyclostomes, or lampreys and

hags, and on the other hand, the gnathostomes, or jaw-bearing vertebrates, comprising true fishes, amphibians, reptiles, birds and mammals (including man)."

In view of the above statements, it seems a little puzzling that Gregory did not give more consideration to the ammocoete in the basic phylogenetic position in his scale rather than emphasize the more highly specialized ostracoderms. Presumably he attached considerable importance to the age of these fossil forms and did not care to assume the existence of an unknown soft-bodied animal giving rise to an armored type which became soft-bodied again by losing these parts. But certainly the type of exoskeleton possessed by ostracoderms is not in line with advanced phylogeny, unless the armor plates are regarded as forerunners or homologs of the smaller and more numerous scales of other fishes. One might consider the possibility that some early chordates passed through the complete age of ostracoderms without developing parts to become fossilized.

The backward character of the ammocoete eye might appear to be discordant in an archetype. The same is true with reference to the dorsally located and atypical naso-pituitary opening similarly placed in the ostracoderms. We shall first consider the eye.

A curious and generally unknown phase in the development of the eye of ammocoetes may have phylogenetic significance. In his exhaustive study of "The Vertebrate Eye," Walls (1942) redescribed a patch of functional visual cells which develop embryologically in ammocoetes as "Retina A," but lose their function when the young larva burrow in the sand and mud. Then at metamorphosis (several years later) "throughout the remainder of the much expanded retina ('Retina B') the visual cells are suddenly differentiated and the borders of Retina A become indistinguishable. Retina A goes out of function when the young larva first burrow in the mud and the eye is blind until metamorphosis when the skin covering becomes transparent and Retina B matures." Walls

further points out that Stŭdnicka's theory of the primitive eye "laid great stress on the eye of the young larval lamprey which is precociously functional while still merely an optic vesicle, as indicating that the vertebrate eye was originally merely a 'directional' one before it became capable of forming images. Since the lens is already present in the tiny lamprey, but in the form of a flat cushion incapable of dioptric function, Stŭdnicka argued that it must have existed phylogenetically a vestigial remnant of something else, possibly a sense organ before the retina was devised at all." One might speculate on the possibility that the onset of the burrowing habit in ammocoetes represented not only a critical period in the life-history of ammocoetes but also had a significant relation to the subsequent phylogeny of other chordates, which unlike ammocoetes did not burrow in the mud. The appearance, disappearance and reappearance of similar function in a developing organ does not seem to be paralleled among any other vertebrates.

Students of the comparative anatomy of the anterior pituitary have traced this organ phylogenetically to a "hypophyseal pit" on the dorsal aspect of the head of cephalaspid ostracoderms, in a position that corresponds to the nasopituitary opening of modern cyclostomes. The primitive position and extrabuccal origin of the anterior pituitary is reflected in its development in amphibians, in which the anlage moves from an original dorsal position to a more ventral one. These observations indicate that the more usual mode of origin of the anterior lobe in vertebrates (from buccal ectoderm) has been secondarily acquired from an Ordovician ancestral form that possessed a well-developed pituitary complex, and that the condition in cyclostomes is essentially primitive rather than degenerate. Homologous features in acraniates, if present at all, are extremely obscure and must be based on meager and questionable evidence. The comparative anatomy and physiology of the pituitary has recently been reviewed by Gorbman (1941b).

V. Probable Role of Endocrines in Evolution

Development of adequate thyroid tissue would seem to be essential not only to the proper development of the individual but also to the advancement of the entire race of vertebrates. The most striking differences between the endostylar organs of acraniates and ammocoetes involve the number and character of cell types and the gross morphologic pattern. In my analysis (1939) of the homologies in endostylar organs, the types of cells most active in the formation of thyroid follicles in ammocoetes are either entirely lacking in acraniates or have been so altered as to obscure their phylogenetic relationship. Of the six types of cells making up the endostylar apparatus in ammocoetes only two (possibly three) are even present in amphioxus. In functional morphology, the endostyle in acraniates is obviously a ciliated tract concerned with propelling food through the pharynx, whereas the endostyle proper of ammocoetes is to be regarded as a primitive pouch designed for the intake and circulation of water over a large absorptive area. The design in ammocoetes suggests that the organ is utilized to absorb essential dissolved minerals from the water which may be concentrated and stored in its tissues (Leach, 1939). Despite text-book repetition, there is no clear functional agreement between the endostyle of amphioxus and that of ammocoetes, and the usual statement that the endostyle of ammocoetes is phylogenetically intermediate between the acraniate endostyle and the thyroid of true vertebrates is to be seriously questioned. The view that the endostylar apparatus in all acraniates are specialized remnants of an earlier generalized structure leading directly to the vertebrate thyroid would appear just as valid and understandable.

Recently, Gorbman (1941a) has shown that the endostyle of the ascidian, *Perophora annectens,* does not store iodine but that the stolon is capable of iodine accumulation in a degree comparable with vertebrate thyroid. He, with Dr. Creaser (1942), has further shown that the endo-

style of ammocoetes does accumulate iodine; and that the endostyle of amphioxus and of two other ascidians do not. The circumstance that the stolon of the ascidian is a reproductive organ and usually arises in ascidians from the pharyngeal endoderm in the region of the endostyle is of particular interest. I have frequently observed migrating germ cells in the mid-dorsal fold of the pharynx of ammocoetes above the epipharyngeal groove, which is a part of the endostylar complex. This may be a morphologic clue to the functional relation of the thyroid to the reproductive glands.

VI. Discussion

The few experimental studies which have been made on the endocrines of the lower chordates have yielded few important positive results. My own observations (unpublished), together with those of others, show with certainty that ammocoetes do not respond to thyroid treatment after the manner of amphibian larval forms either as to metamorphosis or metabolism. But, as was previously set forth, the larval lamprey is not provided with similar structure, so that parallel results from similar treatment should scarcely be expected. My opinion is that the endocrine glands, such as the thyroid and anterior pituitary, which possess multiple properties have developed their fractions or properties progressively and phylogenetically and that these properties operate only in particular combinations. Although there is little experimental evidence to support this view, some significance may be attached to my observations that normal metamorphosis occurs in lampreys without any increase in oxygen consumption. Thus one may assume that a fraction of thyroid concerned with metabolism is either not fully developed or that the lamprey is capable of responding only to fractions concerned with growth and metamorphosis, and to the latter only at a critical and peculiarly delayed period in the life history. Recent observations by Smith and Everett (1943) support earlier opinions that the met-

abolic property of thyroid is also not present in teleosts. Etkin (1934) also presented data discordant with the usual opinion that the thyroid gland produces an increase in the oxygen consumption of frog tadpoles but used a different basis of computation than previously used. These studies would appear to be of phylogenetic interest.

This review should not serve to discredit amphioxus with reference to its clearly primitive characters and simplicity of structure. To accept it as an archetype of the vertebrates, however, seems to be a different matter and requires more detailed analyses than have been made. The review definitely supports the opinion that amphioxus should be regarded as a persistent and paedogenic larval form that has undergone a considerable amount of so-called degenerate specialization probably associated with its burrowing habits. To the believer in the recapitulation hypothesis who follows through the complete developmental history of amphioxus, the conclusion would certainly be reached that many periods occurred in its phylogeny when "it had no idea as to which tree it was climbing."

Incidently, the present paper should add emphasis to the recognized need for a modern and extensive monographic account of the lampreys which would include a redescription of the detailed morphology of ammocoetes and a full account of the transformation process. Many of the difficulties one encounters in working with these animals, along modern lines, is referable to the uncoordinated and often fragmentary information that has been published concerning them and the necessity of getting much of it first hand.

Summary

(1) A review of the opinions of leading students of comparative anatomy and phylogeny of the vertebrates shows that they were remarkably consistent in regarding amphioxus as an unsuitable archetypal chordate, and looked upon it as a degenerate type entirely off the line

of vertebrate evolution. This is discordant with most text-book accounts.

(2) Much of our information concerning ammocoetes has been used by investigators of phylogeny in constructing an idealistic archetype acceptable to them as a chordate connection with invertebrate progenitors. The unpopularity of the various hypotheses is apparently responsible for the present lack of knowledge of the ammocoete and its archetypal characters.

(3) Physiological evidences support the view that amphioxus is extremely degenerate. From a review of studies on organizers and endocrines, the morphologic characters of amphioxus are remarkably similar to a predicated condition based on analogies from experimental work.

(4) The conclusion is made that a sequence of dependent events occurred in the phylogeny of amphioxus initiated by the loss of head parts.

(5) Loss of the pituitary is regarded as particularly significant in leading to a degeneration of the thyroid gland (endostylar complex). Degeneration of thyroid apparatus is reflected in the peculiar development of amphioxus and morphologic deficiencies of acraniates in general.

(6) Since the thyroid gland is so characteristic in all vertebrates and largely responsible for the regulation of growth, differentiation and metabolism of higher forms, its preclusion of function would terminate advancement in phylogeny as in ontogeny.

(7) The review proposes that endocrines possessing multiple properties of independent character have developed these fractions phylogenetically and in a progressive manner. This hypothesis has not been tested very fully.

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GEOGRAPHICAL DISTRIBUTION OF THE GENUS *PYRUS* AND TRENDS AND FACTORS IN ITS EVOLUTION

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ACCORDING to paleontological data, the genus *Pyrus* (the pear proper) is of Tertiary or, possibly, even more ancient origin. Tertiary remains (leaves) have so far been found only in a few localities of western Europe and the Caucasus. In western Europe—in Miocene deposits at the famed site of Tertiary remains, the village of Parschlug in Steyrmark, Austria—Unger found and described the fossil species, *Pyrus theobroma.* In the Caucasus, according to Palibin, *P. theobroma* is found in eastern Georgia in the Kakhetia Mountains in Middle and Lower-Middle Sarmatian deposits, together with representatives of a mixed flora including a considerable number of evergreens, which attests a subtropical or, at least, a warm climate. *P. communis* L. is found in eastern Georgia in Upper Pliocene deposits in the Akchagyl horizon and in Azerbaidzhan in the Apsheron horizon. In all cases these fossil remains are found among representatives of a warm, temperate climate, together with numerous species identical to present-day forms. Post-glacial remains of the pear (fruits) are known in lacustrine deposits in Switzerland and Italy.

In contrast to the closely related genera, *Malus* and *Crataegus,* which belong to the so-called "arctic-Tertiary" flora and have, like other members of this flora, representatives both in Asia and North America, the genus *Pyrus* has no fossil occurrences in North America. This specificity in the location of fossil remains of *Pyrus* and the peculiarities of the present geographical distribution of the genus indicate that it originated at a later date than the other genera mentioned and in a different geographical region.

The species composition of the genus *Pyrus* has not yet been definitely established. The number of species increases as further special investigations are made. According to the latest taxonomic works,[1] there are as many as 60 different species names for described forms, which number, however—after discarding duplications and reducing many to the rank of varieties—falls to 25. To these there should be added *P. gharbiana* Trab. and *P. mamorensis* Trab. (from North Africa) and a number of new species discovered in recent years in the U.S.S.R.

During the past fifteen years there have been revealed in the Caucasus and Soviet Central Asia centers of remarkable diversity of pears, and there have been discovered several new species in these regions. Voronov has described three new species in the Caucasus—*P. Raddeana, P. taochia* and *P. oxyprion;* Popov—two hybrid species in Soviet Central Asia, *P. Vavilovii;* Maleyev—*P. zangezura* in southern Armenia and *P. turkomanica* in the Kopet-Dagh Mountains; Fedorov—two species in southern Armenia, *P. Grossheimii* and *P. Takhtadjanii* and one species in Lenkoran, *P. Sosnovskii.* During very recent years the writer has described five new species from southern Armenia: *P. elata, P. nutans, P. Voronovi, P. Medvedevi* and *P. complexa.*

After a critical study of the genus there remain at least 35 species, differing from one another in regard to the number of varieties and forms they comprise, the complex of characters they possess and the degree to which these characters are expressed, and their antiquity and areas of distribution.

The species diversity of pears is concentrated in two regions of the globe—western Eurasia and eastern Asia, chiefly China. In these two regions there were formed two distinct groups of species and cultivated forms of pears—western and eastern. The former includes over

[1] C. K. Schneider, Illustr. Handb. d. Laubholzkunde, 1906; Rehder, Manual of Cultivated Trees and Shrubs, 1927; Index Londinensis, 1933.

20 species, found in Europe, northern Africa, Asia Minor, Iran, Soviet Central Asia and Afghanistan. To this group belong most of the cultivated pears of the globe. The second group embraces from 12 to 15 species concentrated in eastern Asia, from the Tien-Shan and Hindu Kush Mountains to Japan. To it belong a very large group of varieties cultivated in China and Japan.

The geographical distribution of the various species shows that the genesis and dispersal of the genus *Pyrus* took place in ancient times over an immense territory, extending from eastern Asia to southern Europe and northern Africa. Taking into consideration the areas of the various genera of *Pomoideae,* it seems very probable that their common progenitor was widely distributed over this territory in the Cretaceous period or, at any rate, in the Paleocene epoch (early Tertiary).

The most probable place of origin of the genus *Pyrus* is the mountainous region (on the border between the north temperate and tropical zones) in western and southwestern China, where, according to recent investigations (Wilson and others), there is concentrated an exceptional wealth of genera and species of *Pomoideae* and *Prunoideae*—a region that may well claim to be the primary center of origin of the floras of Asia and Europe, as Komarov (1908) noted in his work, "Introduction to the Floras of China and Mongolia."

Beginning with the Tertiary period, as has been established, an exchange of floras was possible between Interior Asia (including central Asia), on the one hand, and the Caucasus, Asia Minor and the western regions of the Old World, on the other.

Living evidence of the dispersal and evolution of the genus *Pyrus* in ancient times is found in the form of relict species, at present geographically isolated but characterized by certain common features of a primary character. These include: *P. longipes* Coss.-Dur. in the Atlas Mountains (Algeria and Morocco), *P. Boissieriana* Bse. at

Talysh in the Kopet-Dagh Mountains and *P. cordata Desv.* on the Atlantic coast (France, England), all characterized by fruits having a deciduous calyx, being similar in this respect to the East-Asiatic species, *P. Pashia* Ham.-Don., *P. serotina* Rehd., *P. betulaefolia* Bge., etc. Or let us take another example. The xerophytic species of Anterior Asia and Soviet Central Asia—*P. glabra* Boiss., *P. heterophylla* Rgl. et Schmalh., *P. bucharira* Litw.—and the East-Asiatic species are likewise geographically and especially ecologically isolated, but their affinity is, nevertheless, established by the fact that they possess the following characters in common: dissected leaves, ovary with few locules.

Paleontological remains of the genus *Pyrus* and of closely related genera from the period of the great mountain-forming processes in Asia, Europe and Africa and the connection of the past area of the genus with the chief mountain systems of these continents give grounds for linking the development and dispersal of the genus with the formation and location of these mountain chains. The fact that the latter run east and west led to the genus dispersing in the same direction. Deserts, seas and snow-covered mountains constitute insuperable barriers to the natural dispersal of the genus. Only in foothill and adjacent regions are there found, on the one hand, a great diversity of ecological conditions favoring form-genesis and, on the other, a certain uniformity in average conditions (climatic, edaphic) that makes possible the unimpeded dispersal of forms. Convincing facts in favor of this view we find, for instance, in the distribution and localization of the diverse forms of *P. salicifolia* Pall., *P. elaeagrifolia* Pall., and *P. syriaca* Boiss, in the U.S.S.R.

P. elaeagrifolia grows on the northern and southern foothills of the Crimea, extending on the east to the Kerch peninsula, but it is not found in Novorossisk District, which territorially and floristically is so close to the

Crimea that it belongs to the same botanical province. The steppes and the narrow expanse of the Azov Sea constitute an insuperable barrier to the spread of this species. *P. salicifolia,* which grows in the Caucasian foothills, has extended its range from Armenia into Georgia, Azerbaidzhan and Daghestan, but it is not found either in the steppes or in humid forest regions in the mountains. *P. syriaca* is distributed, in a great diversity of forms, only in the middle altitudinal zone in Zangezur and Daralagez (southern Armenia).

The western group of forms extend as far east as the western Tien-Shan, Pamir and Hindu Kush Mountains. The Himalayas constitute a bridge between the western and eastern regions of species diversity of this genus. Here we find a member of the eastern group, *P. Pashia,* having migrated hither from China. This species, with respect to a whole number of morphological characters, may be regarded as an intermediate link between the eastern and western species. Of all the eastern species it is the closest to *P. communis* and *P. Korshinskyi.*

On the basis of our botanico-geographical study of the genus *Pyrus,* we may draw the following conclusions as to the genetic relations and comparative antiquity of the principal species.

The most ancient species, still preserving primitive features, are the Chinese—*P. serotina, P. Calleryana, P. betulaefolia* and others. *P. Pashia* constitutes a connecting link between the relict species, *P. Boissieriana* and *P. longipes* (which are close to *P. communis*), on the one hand, and *P. Korshinskyi,* on the other. Close to the latter, morphologically and biologically, are the xerophytic species of the Iran group—*P. heterophylla, P. glabra* and *P. salicifolia*—and the species of Asia Minor and the Mediterranean Basin—*P. syriaca, P. elaeagrifolia* and *P. amygdaliformis* Vill. *P. Korshinskyi* is undoubtedly linked with the Iran group by way of *P. heterophylla* and with the Asia Minor group by way of *P. syriaca,* the ex-

ceptional similarity and closeness of which were noted by Litvinov.

The most recent branch in the evolution of each of the three main, primitive groups of pears we consider to be as follows: Group I (Chinese), *P. ussuriensis* Maxim.; Group II (*P. Boissieriana, P. longipes*), *P. communis;* Group III (Iran and Asia Minor), *P. nivalis* Jacq., close to *P. elaeagrifolia,* probably a variety of the latter.

Taking into account the present geographical distribution of *Pyrus* species and the generally accepted views on the chief factors involved in the development of floras, it must be recognized that the evolution and species differentiation of the genus are based primarily on processes of xerophytization and borealization. These processes, particularly the former, have been operative over a prolonged period of time and over great expanses of territory in the southern part of the area of the genus. Hence, the great diversity of species of pears in the region of the ancient Mediterranean. From the beginning or middle of the Tertiary period the extent of dry land in this region began to increase, and there were formed centers of xerophytic forms—Central Asiatic, Iran and Asia Minor. In these centers there developed, corresponding to the diversity of physiographic conditions, a large group of Mediterranean species, to which the Central Asiatic species may also be referred.

The diversity of climatic conditions in this region and their close similarity to those prevailing in ancient times have led, on the one hand, to the creation here of great genotypic diversity and, on the other, to the preservation and development of relict types less specialized genetically. In the Anterior-Asiatic center, particularly in southern and southeastern Armenia (Daralagez, Zangezur), there have been discovered modern centers of species-formation in *Pyrus.* The species, *P. syriaca* and *P. amygdaliformis,* which are found in Anterior Asia and along the shores of the Mediterranean, are in a stage of

intensive form-genesis; due to their polymorphism and morphological instability, they present many difficulties to the taxonomist. The species, *P. salicifolia, P. heterophylla* and *P. glabra,* which are biologically more specialized, are extreme xerophytic types, polarized, so to say, genotypically.

As examples of the effect of the process of borealization we may cite *P. communis* and, probably, several forms of *P. elaeagrifolia* (*P. nivalis* Jacq.). As compared with southern species, the European *P. communis* is characterized by great uniformity. The diversity of this species found in several countries of western Europe, *e.g.,* in France, can not be compared with the polymorphism of *P. syriaca* and *P. amygdaliformis,* and has arisen, no doubt, as a result of hybridization with cultivated forms. It should be noted that even *P. communis* is most polymorphic in Central Asia, Transcaucasia and Asia Minor, *i.e.,* in the region of the ancient Mediterranean. This is confirmed by historico-geographical data. The present-day representatives of *P. communis* in Europe are of comparatively recent origin, and they all arose under like conditions of borealization. The ancient representatives either have died out or have been preserved in the south, where they have undergone a more prolonged period of differentiation under more normal conditions. It is remarkable that it is precisely the Transcaucasian forms of *P. communis* that are closest to the relict species, *P. Boissieriana* and *P. longipes.*

Analogous relations may be observed in the East-Asiatic group of species, with this difference, however, that the process of xerophytism has left less imprint, while the process of borealization has been more prolonged and produced more effect. As a result, in the northernmost part of the area of this group, in Manchuria and the Amur and Ussuri Basins, there has developed a boreal species, *P. ussuriensis* Maxim; in the northwestern part, adjoining the Central Asiatic (Mongolian) arid cen-

ter, there have developed types with xerophytic features —*P. betulaefolia* Bge., *P. phaeocarpa* Rehd.; in the central part, where conditions are closest to those of ancient times, there has developed a large group of species of the type of *P. serotina* Rehd.; and, lastly, in the southern and southwestern part, bordering on the subtropics, a form transitional to the evergreen type, *P. Pashia* Ham.-Don.

P. ussuriensis Maxim. constitutes the most specialized branch of the East-Asiatic group, being characterized by the same degree of elaboration and divergence as most species of the Manchurian flora. This species originated in a more ancient period than the European *P. communis.*

In the present epoch one of the most important factors in species- and form-genesis in *Pyrus* is hybridization. More than six hybrid species have been described. By a study of the wild species in Soviet Central Asia, the Caucasus and the Crimea the writer has established the existence of numerous interspecific hybrids, some of them composite hybrids. In places where areas overlap and where in general there is found the greatest species diversity there is concentrated an amazing diversity of forms of *Pyrus, e.g.,* in southern Armenia and western Tien-Shan.

Particularly great is the rôle of hybridization in the origin of the diversity of cultivated varieties. By a comparative analysis of wild and cultivated forms of *P. communis* it has been found that some cultivated varieties of this species possess characters, particularly leaf characters, indicating the participation in their heredity of other species, *i.e.,* the hybrid origin of ancient types. Thus, as regards the shape and texture of the leaves, the character of dentation of the leaf margin, and the size, color, shape and pubescence of the buds and shoots, in some cultivated varieties of *P. communis* we may detect characters of *P. syriaca, P. Korshinskyi, P. salicifolia* and *P. elaeagrifolia.* A number of cultivated varieties have in recent times been created by interspecific hybridi-

zation with the participation of *P. ussuriensis* and *P. serotina.*

As a result primarily of natural and artificial intervarietal hybridization, there has developed during the past two centuries an enormous varietal diversity of cultivated pears. For the radical improvement of the pear with respect to winter hardiness, disease resistance and ecological adaptability pear breeders now have at their disposal a great diversity of initial material. In hybridization work there may be utilized representatives of different species possessing valuable biological properties.

Interspecific hybridization, as in the case of other plants, induces intensive processes of form-genesis and accelerates evolution in new directions.

REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In these section reviews and notices of current publications on general biology emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution. Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Mankind So Far. By William Howells. Garden City, New York: Doubleday, Doran and Co. (Am. Mus. Nat. Hist., Sci. Ser., 5), 1944: i–xii, 1–319, 7 pls., 37 figs. $4.50.

It has been said that the anthropologist is most competent to appraise the past, present and future of man. Certainly his appraisal is worthy of consideration, particularly when it is set forth, as it is by Howells, in a thorough yet fascinating way. A particular virtue in this book is the presentation of findings on hominid evolution that were so recently published or so technically presented as to have escaped the attention of all others than specialists, and perhaps some of them.

Principles of phylogeny and speciation are continuously made the basis for judgment on the ancestry of man and on the course of human evolution. This background biology, which is of prime concern to us, is a mixture of good and bad, with the good predominating in matters of real importance. Thus a strong contrast is rightly drawn, as Kinsey did for gall wasps, between the insular and the continental types of speciation in man. The evolutionary potential of the generalized and the limitations of the specialized are often well expressed. Nevertheless, the bizarrely specialized ostracoderms are placed, on the authority of certain leading students of vertebrate evolution, to be sure, near the base of the vertebrate stem leading to man.

The carrying backward of several phyletic lines well

toward the ancient, generalized root, within the human species, within the genus *Homo,* within the Hominidae and within the Primates is quite in line with the trend in phylogenetic research. Yet the course of evolution is repeatedly portrayed as on the plan of a spruce tree, despite the fact that the interpretations preferred would have been much better expressed figuratively by a deliquescent rather than an excurrent tree; even better by many-stemmed shrubs connected by runners. The possible polyphylety of *Homo sapiens* is considered, but hardly favored.

The importance of the natural selection principle in "The Origin of Species" is stressed as Darwin is elevated on a high pedestal, but in the next breath selection is held to be no longer accepted by naturalists generally as the main key to evolution. "There is actually no evidence or explanation," we read, "for the phenomenon of adaptation." Obviously, Howells has failed to appreciate the extent of the swing toward Neodarwinism which has been expressed during the last decade, not only by naturalists, who never wandered far from the fold, but also by geneticists. Evolution, of course, is taken for granted as a fact.

Orthogenesis and Lamarckism are rejected rather thoroughly, but the evolutionary facts which have given rise to such theories are left unaccounted for. The rather ready explanation of these facts on the basis of selection are not given due consideration. There are hints of a predestinational philosophy.

The treatment of anthropological facts appears to be accurate and the presentation of the conflicting theories based on these data seems to be conservative and judicious. Erroneous and doubtful statements noted by the reviewer are largely in biology. We are told, to cite examples, that man is the newest animal; that lungs, warm blood and the human brain are not specializations; that roundworms have been selected, because they are segmented, as ancestral to vertebrates; that amphioxus is only "inch-long"; that the fauna of Celebes is essen-

tially Asiatic. Some of these mistakes could have been eliminated, had a broadly trained biologist read the manuscript. Some minor misstatements are attributable to imaginative and dramatic presentation, which though effective should never be allowed to transgress or distort accuracy, even in details.

Human races are treated at some length. Hybridization is relied upon to explain the characters of many local types, though the modern concept of reticulate evolution is not strongly emphasized. Taking part in the swing away from super-race philosophies, Howells all but denies the existence of any racial differences in mentality. The superficial physical differences between stocks are, even more oddly, ascribed to nonadaptive evolution. In limiting adaptation to specific differences the claims of many biologists are transposed. I favor the view that most racial as well as most specific differentiae are of adaptive significance.

In the final, rather anticlimactic chapter, "1492 to 1,000,000 A.D.," the anthropologist takes a look forward. He foresees the possible further loss of head hair and the chance that man may eventually become bereft of his little toe, but in between almost completely ignores mankind's greatest problem: how to forestall the tendency toward degeneration which, unless somehow checked, may on biological grounds be expected to follow our release from many of the rigors of natural selection.

The Sources of Life. By SERGE VARONOFF. Boston: Bruce Humphries, Inc., 1943: 1–240, figs. 1–47. $3.50.

To Serge Varonoff the sources of life are the glands of internal secretion, particularly the sex glands; they are the seat of energy and well-being; their reduced functioning leads to senility, which, before some such age as one hundred, is pathological and avoidable. The author's remedy is the grafting of endocrine glands, by special techniques that are said to insure the continued function-

ing of the transplanted tissues. For operations on man, the glands of other primates are used.

The critical reader will find many reasons for doubting part of the claims that the hand of time may be turned backward for man by the monkey-gland operation. The attempted demonstration is by the precept of example, without sufficient statistical analysis to make it certain and obvious that the successes recorded are attributable to the grafting of simian testes. Since many of the operations involve the transplantation of the thyroid and other endocrine glands in addition to the sex glands, the particular role of the grafted testes is obscured. Failures up to "5 to 12 per cent." are admitted, and no real proof is given that the average case is substantially benefited. Some of the before-and-after pictures are very striking, but others are less convincing. The one case in which hair is claimed to have been restored is illustrated by photographs of a man who appears much balder after than before the operation (Figs. 38 and 39).

The most spectacular claim, from a biological standpoint, is that the offspring of grafted rams yield an increased amount of wool. In Algeria the sheep thus magically endowed with hair-growing power are claimed to be the only ones that grow wool on their bellies. These are among the few claims supported by actual figures, but the data are hardly precise. Dr. Varonoff envisions an enormous increase in the wool crop through gland operations on the rams. "We are at the dawn of a new era," he exuberates, for he expects to "create, by grafting, a new race endowed with longer and more abundant wool." He makes no definite claim that the human race can be similarly improved through gland transplants on men, but he hints at such a belief in quoting the experience of a disciple. The spectacular results which he has obtained with thyroid transplants on myxoedematic idiots seem unquestionable. That the energy of senile animals and even their reproductive capacity have been restored and carried several years beyond the normal span of life

seems proved for at least some of the gland operations, but to accept the claim that the descendants of a grafted male will be greatly affected stretches the biological mind beyond the limit of elasticity.

The demonstrated persistence and long-continued functioning of some of the simian gland transplants in man provides further evidence of the close relationship between *Homo* and the great apes and other primates.

Dr. Varonoff writes with convincing sincerity, rising occasionally to the spirit of a Messiah: "I have responded to the needs of the world. I have opened a new prospect." His convictions are obviously so strongly rooted as to push aside, at times, the firm ground of scientific criticism.

Notices of New Books

Elements of Biology A Brief Course for College Students. By Perry D. Strambaugh and Bernal R. Weimer. New York: John Wiley and Sons, 1944: i–vii, 1–461, figs. 1–208. $3.25.—"Of the making of biology textbooks," the authors admit, "there is no end." In this one, "there are two general objectives. First, there is the presentation of certain basic principles. . . . Second, there is the incorporation of the fundamental information that will contribute to better living and more efficient participation in the affairs of society." In these worthy aims the authors have been successful. It is clear that "integration of the material used has been obtained by lining up the facts on a functional thread," but the authors have not consistently "followed the pedagogical course of proceeding from the known to the related unknown." The first factual material, on the physico-chemical constitution of matter, on cell structure, and on plant physiology is not ground that the elementary student has trod. Classification is almost eliminated, and I am particularly disappointed to find only a dozen lines on fishes. Although applied biology is commendably stressed, conservation is very inadequately treated. The discussions of soil erosion, conservation of water, and forestry are very brief, and the treatment of wildlife is even less adequate, for it is confined to eleven lines and leads off with the disproven idea that forests are "the natural home of wild life."

A Text-Book of Histology Arranged upon an Embryological Basis. Sixth Edition. By J. LEWIS BREMER. Rewritten by HAROLD L. WEATHERFORD. Philadelphia: The Blakiston Co., 1944: i–ix, 1–723, figs. 1–598. $7.00.—This splendid text has had a long and respectful lineage. The first edition, by Frederic T. Lewis, was a free translation of Phillip Stöhr's Lehrbuch der Histologie. The third to fifth editions were rewritten by J. Lewis Bremer. Now Harold L. Weatherford carries on, bringing the material up-to-date and adding more than three hundred new figures, many in color. The two previous authors and other colleagues at Harvard aided Dr. Weatherford in the large task of revision. The result is a comprehensive, finely illustrated and well-documented treatment of normal human histology.

Conservation in the United States. Second Edition. By A. F. GUSTAFSON, C. H. GUISE, W. J. HAMILTON, JR., AND H. RIES. Ithaca, New York: Comstock Publishing Co., 1944: i–xi, 1–477, figs. 1–236. $4.00.—The Cornell text on conservation has been revised to align it with new conditions and to incorporate new practices. It is a well-rounded, authoritative treatise, clearly presented, neatly printed and embellished by many fine illustrations. The treatment of wildlife, including the fisheries, is more nearly adequate than it is in most books on conservation.

Talk About Wildlife For Hunters, Fishermen and Nature Lovers. By ROSS O. STEVENS. Raleigh, N. C. (privately published by author, North Carolina State College, Raleigh, N. C.), 1944: 1–229, frontisp., figs. 1–97. $3.50 (cloth), $2.25 (paper).—With particular emphasis on the organization and functioning of state conservation agencies, Professor Stevens talks about wildlife, illustrating his ideas with cartoons and photographs. There is still much need for the improvement of wildlife administration, and for the crusading spirit which the author repeatedly exhibits, but the transcendent importance of competent personnel is perhaps not fully appreciated. Research, education, and restoration are properly stressed as leading items in the reform of wildlife affairs.

Studies on the Pacific Pilchard or Sardine (Sardinops caerulea). By OSCAR E. SETTE and Others. U. S. Fish and Wildlife Service, Special Scientific Reports Nos. 19–24, 1943: 173

pp., 2 pls., 49 figs. Processed.—These reports have a significance that may be partially lost because of the place and method of publication. They deal with the design of a research progam in conservation; problems of age and growth; the relation of temperature to the rate of development of eggs; methods of analyzing the size of natural populations, particularly of computing mortalities and replacements; and the distribution of eggs and larvae in reference to temperature and light.

Smoky Ridge. By FREDERIC DOYLE. New York and Toronto: Longmans, Green and Co., 1944: i–vii, 1–128, 10 pls. $2.25.—In simple and charming style, individualizing but not personifying the characters, the author of this little book presents chapters in the drama of animal life along the Smoky Ridge. The basic natural history is essentially sound, though a few general misconceptions are repeated, as when the black bear scoops a fish out of a stream and onto the bank with a swing of its paw.

AMERICAN SOCIETY OF NATURALISTS

THE new officers of the American Society of Naturalists, elected by mail ballot in place of the annual meeting which would have been held in December, 1943, are: *President,* Dr. FAY COOPER COLE (Anthropology), University of Chicago; *Vice-President,* Dr. CHARLES W. METZ (Zoology), University of Pennsylvania; *Secretary,* Dr. WM. RANDOLPH TAYLOR (Botany), University of Michigan; *Treasurer,* Dr. M. R. IRWIN (Genetics), University of Wisconsin (continuing); *Editorial Board,* THE AMERICAN NATURALIST, Dr. LEON J. COLE, Dr. A. FRANKLIN SHULL and Dr. LAURENCE H. SNYDER.

The society will meet with the American Association for the Advancement of Science in Cleveland, September 12–14, 1944. It is planned to hold the Biologists' Smoker on the evening of September 12, a Symposium and Business Meeting, probably on the afternoon of the 13th, and the Annual Dinner and Presidential Address on the evening of the 14th. The official headquarters for the society will be the Hotel Statler.

WM. RANDOLPH TAYLOR

THE CHARLES BENEDICT DAVENPORT MEMORIAL FUND

Dr. CHARLES B. DAVENPORT, whose death occurred on February 18 of this year, had served from 1898 until 1923 as director of the

Biological Laboratory, and from then until his death as secretary of the Long Island Biological Association. At a meeting of the Executive Committee of the Board of Directors, in the latter part of February, a resolution was passed expressing a sense of irreparable loss in the death of Dr. Davenport, who, to a greater extent than any other individual, was the founder of the Biological Laboratory. Among all his fellow workers and neighbors his memory will stand not only for high attainment but also for an abiding example of integrity, helpfulness and warmth of heart. The Executive Committee decided at that meeting to ask the members of the association, as well as friends and colleagues of Dr. Davenport, to contribute toward the establishment of a fund in his memory, the interest of which should be used for aiding scientific research in the biological field. Checks or other contributions in the form of government bonds or securities for the Charles Benedict Davenport Memorial Fund should be made payable to the Long Island Biological Association, and addressed to the Biological Laboratory, Cold Spring Harbor, New York, or to Mr. Marshall Field, Treasurer, Huntington, New York. Contributions made to this fund are deductible for income tax purposes.

SHORTER ARTICLES AND DISCUSSION

HETEROCHROMOSOME FORMATION IN THE GENUS *ILEX*

DURING an investigation of some American species of the genus Ilex, several interesting phenomena were studied, among the meiotic chromosomes in microsporogenesis. The sexual habit of this genus is not stable, even though many forms are functionally dioecious. Polygamous specimens and individual trees which change from female to perfect to female types during and immediately following transplanting are not uncommon. It is a moderately large genus—Engler and Diels set it at 280 species limited mostly to the American hemisphere—and contains both evergreen and less familiar deciduous varieties. Since the genus is obviously evolving toward a strictly unisexual condition and is represented by about 20 species in the eastern United States, some of which are certainly quite closely related, two evolutionary trends appear to be present in the same genus, namely, a trend from perfect to the dioecious state and the trend of recent interspecific hybridization. A study of the interplay of two such trends gave promise of results. The observations to date are encouraging, and this initial investigation may stimulate further work by cytologists to whom material of the great majority of species in this genus is readily accessible in North and South America.

A number of plants from each of five species of Ilex were studied and in all these some meiotic abnormalities were discovered during microsporogenesis. In some respects these peculiar chromosomes display characteristics frequently associated with the conventional conception of sex chromosomes, and yet other criteria of sex chromosomes are absent. Therefore the term *heterochromosome* will be used with the connotation that such chromosomes as deviate either from the behavior of the remainder in the complement or from the structure or behavior, or both, of its synaptic mate are called heterochromosomes. The anomalies found in each species are summarized as follows:

Ilex decidua Walt. (n—20). Some precocious chromosomes and occasional anaphase bridging during the heterotypic division. Lagging of several chromosomes and ejection of one anaphase chromatid during second meiotic division in about 50 per cent. of PMCs. No extruded chromatin survived into microspore formation. Evidence of heterochromosomes present.

I. monticola Gray (n—20). Slight lagging during late anaphase of first meiotic division with one chromatid of smallest chromosome consistently ejected into cytoplasm just prior to telophase of first division. Ejected chromatid attempts precocious second division, which does not succeed. In about half of the PMCs, the ejected chromosome is left out of the daughter nuclei and degenerates in the cytoplasm at conclusion of the regular second meiotic division. Heterochromosome in this instance is the smallest member of the complement.

I. opaca Ait (n—18). A medium-sized chromosome is precocious as to division but laggard in migratory ability and often remains at the equatorial plate at the conclusion of the heterotypic division. It undergoes no further division during the second meiotic division and is left to degenerate in the cytoplasm of about 50 per cent. of the PMCs. Frequently half of this heterochromosome is accepted by one of the daughter nuclear groups.

I. verticillata (L.) Gray (n—18). There is one very small chromosome in this species which appears to be tripartite, $X—Y_1–Y_2$, with one terminal section larger than both the smaller units together. This chromosome is often ejected into the cytoplasm as is one chromatid of a medium-sized pair and degenerates during first telophase, which is unlike behavior in other species. These unusual events were found in about half the PMCs, meiosis in the remainder being quite normal in every visible respect.

I. vomitoria Ait (n—20). The single minute chromosome in this species is normal and no ejected chromatin was found in any PMCs. A tripartite complex appears during heterotypic metaphase, but the chromosomes are too small to follow the history of this complex with any degree of accuracy. The complex is laggard during both metaphase and anaphase, almost completing an anaphase bridge, and in some instances indicated a 2–1 separation.

There is no evident uniformity in meiotic behavior among the five species investigated. The chromosome number is aneuploid, but 20 might prove to be the common haploid number since four larger chromosomes were quite often associated during the heterotypic metaphase and may indicate that originally the basic number was five. The pollen in all the species investigated appears to be structurally perfect, although there seemed to be a difference in the rate of maturity as demonstrated by some anthersacs wherein approximately half the microspores contained a dense cytoplasm which took a deeper stain than the remaining spores.

The presence of lagging or precocious chromosomes, occasional anaphase bridging of chromosome complexes, the ejection of chromatin from the spindle and its presence in the cytoplasm during telophase, the resulting variation in chromosome complements of the microspores, all such phenomena are reminiscent of meiosis in plants of hybrid origin. Although the abnormalities in the case of these five species of Ilex are not so violent as to

jeopardize the fertility of the plants, yet they indicate that interspecific hybridization has extended through the eastern North American species in the past and has undoubtedly contributed to the multiplication of species. The presence of active hybridization in relation to the trend towards unisexuality in the genus Ilex may be better understood when compared with the situation found in a genus such as Thalictrum, which contains both perfect, polygamous and strictly dioecious types. The genus Thalictrum is vastly polyploid, with haploid numbers ranging from 7 to 70. The distribution of these numbers includes species with both high and low numbers native to all continents in the northern hemisphere and no distinction can be made between the perfect and dioecious types on the basis of chromosome number. The author wishes to add several new numbers to the array for which Langlet and Kuhn are largely responsible. Meiosis is quite normal in these species: as determined from collections made in Buncombe and Madison counties in western North Carolina.

Thalictrum clavatum	n— 7
Th. dioicum	n—14
Th. polygamum	n—42
Th. coriaceum	n—70

The extensive polyploidy accompanied by regular meiosis, so well displayed by the species of Thalictrum, is generally conceded by cytologists to be the consequence of previous hybridization. However, in this genus it is obvious that polyploidy occurred before the genus moved from the hermaphroditic habit since unisexual as well as perfect types possess the basic number of 7 as well as many of the higher haploid numbers. In other words, unisexuality has not affected the meiotic process at all. The situation is markedly different among the species of Rumex where in the hermaphroditic Eulapathum section there is vast polyploidy and normal meiosis in contrast to the dioecious Acetosa section where aneuploidy is accompanied by irregular meiosis. Thus we may conclude that in the case of Thalictrum interspecific hybridization came first and then the later advent of the unisexual state in some species. Although the evidence is still fragmentary, the situation is otherwise in Ilex. Here the chromosome evolution has been held to a very limited aneuploidy and in recent times probably a negative evolution through the loss of chromatin. Because each act of fertilization also becomes an act of hybridiza-

tion in dioecious heterozygous types, meiotic abnormalities appear to be able to persist over a period of many generations. Although there probably is no uniform quantity of time required for the evolution of the unisexual habit, the absence of strictly perfect species in Ilex suggests that the dioecious condition is much older in species of Ilex than in Thalictrum. One might therefore conclude that the occurrence of heterochromosomes in Ilex lies in the unique combination of hybridization and the advent of unisexuality at approximately the same time in the phylogeny of the race. Investigators who seek the origin of sex chromosomes among higher plants are limited to phenomena akin to such as are found in the five species of Ilex as the only general and natural source of meiotic disturbance capable of providing the mechanism and the ability to survive through many generations. Laboratory treatment of specimens in order to produce similar vagaries lacks the asset of pertinency possessed by natural types which display these anomalies. The heterochromosomes described for species of Ilex are not sex chromosomes. However, they do supply intermediate steps between autosomes and the X–Y or X—Y_1–Y_2 types and provide us with a rational basis for further investigation on a host of plants which, like species of Ilex, have been subject to both previous hybridization and a change of sexual habit.

The question of survival of these meiotic irregularities through several generations and their adoption as a general characteristic of the species presents an interesting point for speculation, particularly in regard to the presence of heterochromosomes in species of Ilex. As with so many other biological problems involving inheritance, two alternatives offer themselves and our choice will certainly affect our subsequent point of view on details of chromosome evolution. On the one hand we may conceive of a unique meiotic irregularity (a heterochromosome, for example) occurring in one set of chromosomes somewhere in the sporogenous tissue of one plant of a given species. This unusual chromosome must impart two attributes to the offspring of the plant in which the heterochromosome has been incorporated through a previous successful fertilization. First of all, it must impart the ability to insure the survival of this heterochromosome through successive reduction divisions. It must also impart to the offspring a competitive advantage over neighboring members of the same species so that the offspring of the neighbors are gradually eliminated from the main line of descent for the race while the

offspring of the heterochromosome bearing plant gradually usurp the earth afforded the species.

On the other hand, we may conceive of general trends such as hybridization and the assumption of the unisexual habit as forces which affect great numbers of a given population more or less simultaneously over a wide ecological area. These forces would cause unique chromosome mechanisms to arise in many individuals and because of their common distribution within a given species and their similar evolutionary direction they would be able to survive on a broad front. With this conception the necessity for a competitive advantage accruing to the individuals possessing the heterochromosome is not nearly as exacting as in the first hypothesis. The first alternative appeals to the cytogeneticist because it offers a neat mechanism which can be tested under laboratory conditions and appears to be parsimonious with broad assumptions. The second, however, appeals to the ecologist, the systematist, the comparative anatomist who seeks an explanation of things as they grow in the fields in profusion and are scattered around the earth. Perhaps this is another facet of the macro-micro-evolutionary dispute. This is not the place to elaborate the issue, but merely indicate that in the case of the five species of Ilex the meiotic abnormalities would tend to diminish the chromosome number, which does not appear to be the case. This suggests that the nuclei which effect fertilization come from microspores which have the full complement, the half of the PMCs which were regular in meiosis. Yet the ability to disturb the meiotic process sufficiently to produce the heterochromosomes must then be passed on through either the PMCs which do not display it or through the female side. In either event we have a possible means of carrying a meiotic peculiarity from one generation to the next without materially affecting the fertility of the individuals and yet affording a unique chromosome complex out of which so-called sex chromosomes might eventually arise.

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A RELATION BETWEEN CHROMOSOME SIZE AND B VITAMIN CONTENT OF RAT ORGANS

THIS preliminary report deals with a chromosomal differentiation of rat organs that is apparently concerned quantitatively with B vitamin concentration, probably through the mediation of enzymes produced by the chromosomes.

It has been conjectured that enzymes or their specific active groups are exact replicas of genes (Wright, 1942). Antigens are produced under the influence of one or a few genes (Irwin and Cole, 1936; Irwin and Cumley, 1943), and their production has likewise been conceived as a modeling synthesis similar to that imagined to occur in the reproduction of genes (Haldane, 1937). Caspersson (1941) has come to the view that, while heterochromatin produces the histones and ribonucleic acid of the nucleolus, the euchromatin synthesizes "higher" proteins.

Recently the isolated nuclei of rat liver have been shown to contain a number of enzymes. Dounce (1943) has demonstrated arginase, cytochrome oxidase, esterase, lactic acid dehydrogenase, alkaline phosphatase and acid phosphatase, while Lan (1944) has found *d*-amino acid oxidase, uricase and choline oxidase in isolated nuclei in activities approaching their activities in whole liver. The finding of Isbell, Mitchell, Taylor and Williams (1942) that in isolated nuclei of beef heart and of mouse cancer there are appreciable quantities of the B vitamins suggests the presence intranuclearly of enzymes that contain these vitamins within their prosthetic groups.

It is therefore of interest that the size of chromosomes in various normal rat organs should be closely paralleled by the total concentration of the B vitamins, thiamin, riboflavin, nicotinic acid, pantothenic acid, pyridoxin, biotin and folic acid. From acetocarmine preparations made according to the method of Painter (1939) 25 metaphase figures in each of a number of rat organs were drawn under oil immersion with a camera lucida. The drawing magnification was 3,000. The average volume of chromosome per metaphase was calculated by a method previously described (Biesele, Poyner and Painter, 1942). The average chromosome volumes given below are for organs of an 84-day-old male Wistar rat, with the exception of the adrenal gland, that was taken from an adult male Osborne-Mendel rat in which the liver and kidney chromosomes agreed in volume with those of the

adult Wistar rat. It was found that the organs were arranged in this order according to approximate average chromosome volumes: liver, 1.1 cubic micron; kidney, 0.9 cubic micron; adrenal, 0.7 cubic micron; and lung, small intestine, and spleen, 0.5 cubic micron. Correspondingly, the organs of the adult Wistar rat have the following arrangement in descending order of arbitrary units of total B vitamin concentration: liver, 10; kidney, 6; adrenal, 5; spleen, 3; and lung, 2, according to data given by Mitchell and Isbell (1942), and Taylor, Pollack and Williams (1942). These authors did not assay the small intestine. Inositol was omitted from the calculations of total B vitamin concentration because it seems to be concerned more in phospholipid structure than in enzyme systems (Bollman, 1943). The actual mean values of the average chromosome volumes determined, together with their standard deviations, are spleen, 0.46 ± 0.10; small intestine, 0.50 ± 0.12; lung, 0.51 ± 0.11; adrenal, 0.72 ± 0.13; kidney, 0.93 ± 0.26; and liver, 1.12 ± 0.31 cubic micron. Although the first three values are not significantly different statistically, every other possible pair differs significantly except for the kidney and liver, in which, however, the difference between the means is between 2 and 3 times its standard deviation. There is a statistically significant difference, furthermore, between 1.02 ± 0.27 cubic micron, the mean of the average chromosome volumes of 237 metaphases of the livers of 7 adult male rats, and 0.89 ± 0.21 cubic micron, the mean of the average chromosome volumes of 50 metaphase figures of the kidneys of 2 adult male rats.

Embryonic rat liver has about half the B vitamin concentration of adult liver (Williams, Taylor and Cheldelin, 1941), and the activities of a number of its enzyme systems are considerably lower than those of adult liver (Greenstein and Thompson, 1943). Correspondingly, the liver chromosomes of a newborn male Wistar rat were found to average 0.72 ± 0.16 cubic micron instead of 1.12 ± 0.31 cubic micron as in the liver of the older rat. Chromosomes have the same range and frequency of sizes in regenerating and control livers of the rat (Biesele, 1944), and according to Greenstein and Thompson (1943) enzyme activities in regenerating livers are in good agreement with those in normal adult rat livers.

Perhaps the best interpretation to give at present to the direct relation between average chromosome volume and B vitamin con-

centration in rat organs is that the development of the chromosomes, as seen in metaphase of mitosis, is an indication of the total synthetic activity of the chromosomes in producing protein apoenzymes that combine with vitamins and thus determine the bound vitamin capacity of the organ. While the probable importance of cytoplasmic synthesis of proteins and enzymes is not to be denied, it is desired to emphasize that differentiation of the cell may proceed in part through differential synthetic activity of the chromosomes and genes.

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OVARIAN ACTIVITY OF *XENOPUS LAEVIS* WHILE IN CAPTIVITY[1]

Owing to the recent widespread clinical use of *Xenopus laevis* (South African clawed frog) in human pregnancy diagnosis, many reports have been forthcoming regarding the physiology of ovulation in this unusual amphibian. In the test for pregnancy, *Xenopus laevis* extrudes ova within six to twelve hours following injection of urine containing gonadotropic hormones characteristic of pregnancy.

It was at first thought that captivity caused atrophy and involution of *Xenopus laevis* ovaries. Numerous investigators have since shown that ovarian activity continues in captivity, provided, however, that optimum conditions with regard to food, environment and housing are maintained. Aronson (1944) in a recent paper seems to doubt the continued activity of *Xenopus laevis* in captivity, stating that "there is no reason to believe that these toads (*Xenopus laevis*) constantly ovulate." He offers no concrete evidence to support his statement except the work of Berk (1939), who found a seasonal variation in ratio of the weight of the gonads to the body weight of *Xenopus laevis*. Berk, on the other hand, studied these animals in their natural habitat in South Africa.

Having studied these frogs in captivity over a period of five years, our findings consistently agree with the accepted belief that ovarian activity in *Xenopus laevis* continues throughout the year (Weisman and Coates, 1944). The following experiments will show that ovulation in *Xenopus laevis* is unquestionably continuous while in captivity.

Experimental Part

Studies with injections of chorionic gonadotropic hormones: Over a period of four years we have constantly injected *Xenopus laevis* with crude extracts of the urine of pregnant women. Two thousand frogs were so treated during 48 consecutive months. Of these animals, 98.9 per cent. reacted within six to eighteen hours by extrusion of hundreds of mature ova. The remaining few non-reacting animals were injected a second time with more potent extracts, and in each instance a positive egg-extrusion reaction was noted. In other words, if the dosage of the hormone is sufficiently high no healthy female *Xenopus laevis* ever failed to extrude ova following such gonad stimulation.

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Studies of ovaries of animals autopsied: During the course of our research 38 frogs died instantly from either a technical error in injection or a toxic hormone concentration. These animals were all autopsied and studied for gonadal activity. All the frogs were found to contain thousands of ova in various stages of maturation. The autopsies were performed whenever the animals chanced to die and the records of our autopsies indicate that at least one dead animal was studied each month. We have never found *Xenopus* ovaries atrophic or anovulatory.

DISCUSSION

From the preceding experiments, it is at once evident that *Xenopus laevis* differs from *Rana pipiens* and other common American frogs. Regardless of the season of the year, *Xenopus laevis* can be said to be constantly ovulating as shown by its consistent rapid egg-extrusion response and the state of the ovaries at autopsy. *Rana pipiens,* on the other hand, does not respond to gonadotropic activity except during its normal egg-laying period and then only to tremendous doses of gonadotropic stimulation.

SUMMARY

Two thousand *Xenopus laevis* were injected with extracts of chorionic gonadotropic hormones. In every instance, and regardless of the season of the year, egg-extrusion followed potent hormone stimulation within six to eighteen hours.

Thirty-eight animals were autopsied and the ovaries studied for gonadal activity. Each animal showed definite evidence of continuous ovarian maturation and activity.

Regardless of the time of year, *Xenopus laevis* constantly carries ovaries filled with ova in various stages of maturation. Hundreds of these ova are brought to full maturity within six to eighteen hours following artificial gonadotropic hormone stimulation.

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